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Using MORPHOMETRICS, Phylogenetic Systematics and Parsimony Analysis to Gain Insight into the Evolutionary Affinities of the Calymenidae Trilobita

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USING MORPHOMETRICS, PHYLOGENETIC SYSTEMATICS AND PARSIMONY ANALYSIS TO GAIN INSIGHT INTO THE EVOLUTIONARY AFFINITIES OF THE CALYMENIDAE TRILOBITA

Reexamination of the Representative Trilobita Genera, including
Reevaluation and Reclassification of a Common Trilobite, "Calymene" *celebra*
from the Silurian Carbonate Deposits of Southwestern Ohio,
and Systematic Revision of the Family Calymenidae

A thesis submitted in partial fulfillment
of the requirements for the degree of
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By

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Alex Joseph Chestnut ENTITLED Using Morphometrics, Phylogenetic Systematics and Parsimony Analysis to Gain Insight into the Evolutionary Affinities of the Calymenidae Trilobita BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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ABSTRACT

Chestnut, Alex Joseph. M.S., Department of Earth and Environmental Sciences, Wright State Universiy, 2008. Using Phylogenetic Systematics and Parsimony Analysis to Gain Insight into the Evolutionary Affinities of the Calymenidae Trilobita.

The most common trilobite in the Silurian carbonates of Ohio – especially the Springfield Dolomite – is a species that has been assigned to at least five genera over the past 100 years. This trilobite has been variously referred to as *Calymene celebra, Apocalymene celebra, Flexicalymene celebra, Gravicalymene celebra,* and *Sthenarocalymene celebra*. Reexamination of the species *"Calymene" celebra* through parsimony and morphometric analysis was conducted to properly place this calymenid species within the correct genus. What compounds the confusion is that the characters used to seperate the genera within the family Calymenidae, and therefore create the basis for the argument to create a new genus, seem weak at best. Coupled with the use of incomplete specimens in the new descriptions, overinflation of genera is not only possible, but a reality.

In the past 75 years, the pioneers of trilobite research have labored extensively to classify the family Calymenidae. A major study by Shirley in 1936 attempted to classify the calymenids on the basis of cephalic characteristics – specifically the shape of the glabella, variations in the preglabellar field, and the development of papillate lobes – feeling that other morphological characteristics were conservative at best, and unreliable. Subsequent studies have basically followed Shirley's proposed classifications based upon these objective characters. However, a consistant problem with objective character-based analysis is the subjective nature of description.

The purpose of phylogenetic classification (cladistics) is to recognize phylogenetic groups, or taxa, all of whose members are descended from a common ancestor. The common ancestor and all descendents form a monophyletic group. Phylogenetic classification is concerned with grouping

individual species into evolutionary categories. Because classification uses both quantitative and qualitative data, the goal was to remove the subjective nature of qualitative data. By using morphometrics to help find similarities within shapes, description of the cephalon can be defined in absolute values instead of subjective descriptions.

Based on quantitative phylogenetic analysis, *"Calymene" calymene* best fits with *Calymene*, as originally described by Raymond in 1916. Phylogenetic analysis also indicates that the study genera could be "lumped" into the following generic categories (synonymous genera in parentheses): *Alcymene*, *Calymene* (including *Calymene celebra*), *Flexicalymene* (including *Gravicalymene, Nipponcalymene, Onnicalymene, Metacalymene,* and *Sthenarocalymene*), *Diacalymene* (including *Arcticalymene*), *Tapinocalymene*, and *Spathacalymene*.

Landmark analysis was used to corroborate the findings of the cladistic analysis. The graphing of Procrutes fitted cephalic landmarks utilizing Principal Component Analysis and Cluster analysis. Landmark analysis indicates that *"Calymene" celebra* more closely matches with *Calymene* than the other three study genera to which it has been assigned over the past 100 years. These results directly correlate to the findings in the phylogenetic analysis. As additional specimens are added to the data sets and the groups are rerun, the cluster dendrogram from this group shows *"Calymene" celebra* to be more similiar to two other species of different genera. As with the previous data set, *Alcymene, Arcticalymene, Spathacalymene,* and *Tapinocalymene* are outside the main "nesting" arrangement and can be considered different enough to warrant separate generic assignments. However, the remainder of the specimens are too closely nested to warrant individual generic assignment.

When we look at the same data set as used in the cladistic analysis – to include only *"Calymene" celebra* and all genera in the study – the results mirror those when *"Calymene" celebra* is compared to all samples in the study. It was determined that as more samples were added, "Calymene" *celebra* becomes clustered/nested with different genera and/or species, indicating that

the morphological differences between them is not significant enough to warrant division. Analysis of the scatter plots from the Principal Component Analysis of the study genera and *"Calymene" celebra* show that *"Calymene" celebra* always plots closer to *Calymene* than any other genus. In some analyses, they share the same statistical space indicating strong statistical similarities. Because of the strong correlation between both results, we can infer that *"Calymene" celebra* is best assigned to the genus *Calymene*, as first described by Percy Raymond in 1916.

The question remains, what amount of characteristic differences warrant a new genus. Genera should not defined not by one character, but by a group of carefully chosen characters, and in cases where modifications are slight, it is more logical to revise the genus than to create a completely new genus. This would lead us to think that within the genera *Calymene, Flexicalymene, Apocalymene, Gravicalymene,* and *Sthenarocalymene*, as well as others, the morphological characteristics – and modifications of those characteristics – are slight enough that assignment of new genera, as seen over the years was unwarranted.

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PREFACE

Parsimony comes from the latin word *parsimonia*, meaning frugality, and according to current English-language dictionaries, it has two common usages: excessive frugality, and "economy of assumption in reasoning." The initial use of parsimony in a scientific context can be traced to Aristotle, who has been quoted as having said, "God and Nature never operate superfluously, but always with the least effort." While evolutionary parsimony dictates "that nature is fundamentally parsimonious," as scientists, we tend to favor the methodological rule of parsimony, "that parsimony operates by finding a pattern of relationships that is most consistent with the data."

Through the creation of character sets, shape analysis, and computer-based evaluation, the purpose of this study is to find "a pattern of relationships that is most consistent with the data," and in the process, try to answer a fundamental question – to which genus is the calymenid trilobite species *"Calymene" celebra* best assigned, and how can we use this knowledge to reevaluate the family Calymenidae?

ACKNOWLEDGMENTS

A study of this magnitude is not possible without the help and support of the scientific community, faculty, and friends. For all of the pioneers in trilobite research – Adrian, Chatterton, Edgecombe, Eldredge, Foerste, Fortey, Raymond, Salter, Shirley, Whittington, and all of the others – their work has been a over a century of a "labor of love." Without their studies, research such as this, and others to follow, would not have been possible.

Throughout the course of writing this thesis, I came across many quotes from the pioneers that inspired me to continue. I have shared them with you, as lead-ins to each chapter, and occassionally, throughout the paper. In many cases, they are not paramount to the completion of this work, but more a "dedication to the cause." I wanted others to see the driving force behind this work.

I would like to thank my faculty advisors for their invaluable insight and often steering me back on course. A special thanks to Dr. Loren Babcock of Ohio State for sharing his time and knowledge and giving me the opportunity to work with one of the best in the field; and to Dr. Chuck Ciampaglio of Wright State – not only a mentor, but a friend as well – for his enthusiasm when mine wained. Without their support, this project may never have been finished. Many thanks to Dr. Ernest Hauser for sitting on the committee, and to Dr. Songlin Cheng who came aboard at the last minute.

Last, to all of my fellow graduate sudents, especially Angie and Scott, who over the course of the last three years, made going back to school enjoyable.

DEDICATION

Ralph Waldo emerson once wrote, "…To win the respect of intelligent people…To earn the appreciation of honest critics…To leave the world a bit better…This is to have succeeded."

To my family, who stuck by me while I tried to decide what I wanted to be when I grew up, I dedicate this thesis – To Nick, Kris and Kimberly, thank you for being "interested in Dad's work," even though more often you weren't; to Drew, who spent the better part of the last three years sans a father at home; to Becky who picked up the slack and kept things in order; to Jordan who always found fascination in Papaw's "bugs;" to Mom and Dad who taught me that you can never have too much knowledge; and to Susan, who without your constant push, this thesis may never have been written. I owe all of you my heartfelt thanks and gratitude. It is because of you that I have succeeded.

INTRODUCTION

> "Trilobites have a unique morphological and phylogenetic importance, because they are so much the most primitive class within the arthropod phylum. They therefore indicate the mode of origin of this class; indeed, they suggest the nature of the protarthopod and its predecessor the pro-arthropod, and even something of the family relationships of the polychaete ancestor!" (Raw, 1953).

In *Wonderful Life*, Gould describes the Cambrian "explosion of life" and its significance in evolutionary development. Near the end of his book, the first Cambrain fauna – with respect to body design – is refered to as " including a plethora of alternative possibilites, all equally sensible and none leading to us" (p. 316). Gould then proclaims that "once the modern fauna arose in the next phase of the Cambrian, the boundaries and channels were set." Gould stated that it was the arrival of the arthropods, specifically the trilobites, that created an inception of predictability. Because of their great diversity and longevity, Raw stated in 1953 that "trilobites hold an important place in the history of animal life, constituting the dominant fossils at the beginning of the record . . ." (p. 83). From that moment on – at the beginning of the record – the evolutionary "train" was set in motion. What single group of organisms could be more significant in understanding the evolution of life than the trilobite?

The representative trilobite genera in the Silurian bedrock of southwestern Ohio quarries and outcrops has been studied and described in detail throughout the last century and a half by, among others, Hall and Whitfield (1875), Foerste (1919), LaRocque and Marple (1955), Whittington (1971), Ludvigsen (1979), Mikulic (1981), and Gass et. al. (1992). *Acidaspis, Bumastus, Calymene, Cheirurus, Dalmanites, Encrinurus, Flexicalymene, Metroplichas, Sphaerexochus*, and *Trimerus*

have all been identified as a result of these studies. A greater diversity of trilobites in the mid-Silurian of Ohio, much of it previously unreported, is indicated by more recent work in Miami, Preble, and Montgomery Counties. It has been 16 years since the generic diversity has been reexamined and described, and there have been ample new discoveries to warrant it here.

In Silurian carbonate roks of southwestern Ohio, the calymenid trilobite species *"Calymene" celebra* is abundant (see Figure 1). Generic classification and the phylogenetic affinities of *"Calymene" celebra* are uncertain.

Figure 1. Specimens of the calymenid species *"Calymene" celebra* from the Springfield Dolomite, Barrett Paving quarry, Ludlow Falls, Miami County, Ohio.

The common calymenid trilobite trilobite *"Calymene" celebra* has been assigned to at least five genera over the past 100 years: *Apocalymene* (Chatterton and Campbell, 1980), *Calymene* (Raymond, 1916), *Flexicalymene* (Whittington, 1972), *Gravicalymene* (informally by Whittington, 1992), and *Sthenarocalymene* (informally by Holloway, 1980). These multiple generic assignments may have artificially inflated the number of genera reported in literature over the years. Based on published papers on calymenidae trilobites, there is confusion concerning the morphological differences between *Apocalymene*, *Calymene, Flexicalymene, Gravicalymene*, and *Sthenaroclaymene.* Not only is there confusion concerning the identifying criteria, it is compounded by the inability at times to identify such features in the Silurian rocks due to the nature of the preservation. Silurian rocks in southwestern Ohio are primarily dolostones, causing the dissolution

of the exoskeletons. Specimens are preserved as internal and external molds of the dorsal skeletons. There may be a loss of the ome detail (particularly of the external surface) with internal molds, and most of the external molds – the reverses – are destroyed.

New advances in systematics and morphometrics make the reevaluation and reclassification of "*Calymene" celebra* not only possible, but necessary. Once the species *"Calymene" celebra* is reexamined and a reclassification is complete, the same type of parsimony analysis can be made – and should be applied – to the family Calymenidae. Currently, there are 34 genera assigned to the Calymenidae. As with *"Calymene" celebra*, there are other species that have been assigned to multiple genera, or have been reassigned to new genera through the years. Were the criteria used to reassign them sufficient to warrant a new genera? Using parsimony analysis, through morphometrics and cladistics, new insight has been gained and a new systematic scheme is presented.

Location of Study

Previous studies have involved the diversity of the mid-Silurian trilobite fauna from quarries in Miami, Montgomery, and Preble counties, Ohio. All of the field research for this study was peformed at one quarry in Miami County, the Barret Paving quarry in Ludlow Falls, Ohio (see Figures 2 and 3).

The Barrett Paving Quarry exposes the Brassfield Formation (Llandovery Series), as well as strata of the Wenlock and Ludlow Series. Unconformably overlying the Brassfield is the Dayton Formation, and in ascending order, the Dayton Formation is followed by the Osgood Shale, Laurel Limestone, Massie Shale, Euphemia Dolomite, Springfield Dolomite, and the Cedarville Dolomite.

Over the past 15 years, the quarry foreman, Chuck Mills, has amassed a collection of over 2,000 trilobites – many of which belong to the family Calymenidae – from the Springfield Dolomite. The Springfield Dolomite (see Figure 4) is generally described as "an even-bedded grayish-orange dolomicrite or a finely crystalline dolomite" (Ausich, 1987) containing an insoluble residue of quartz

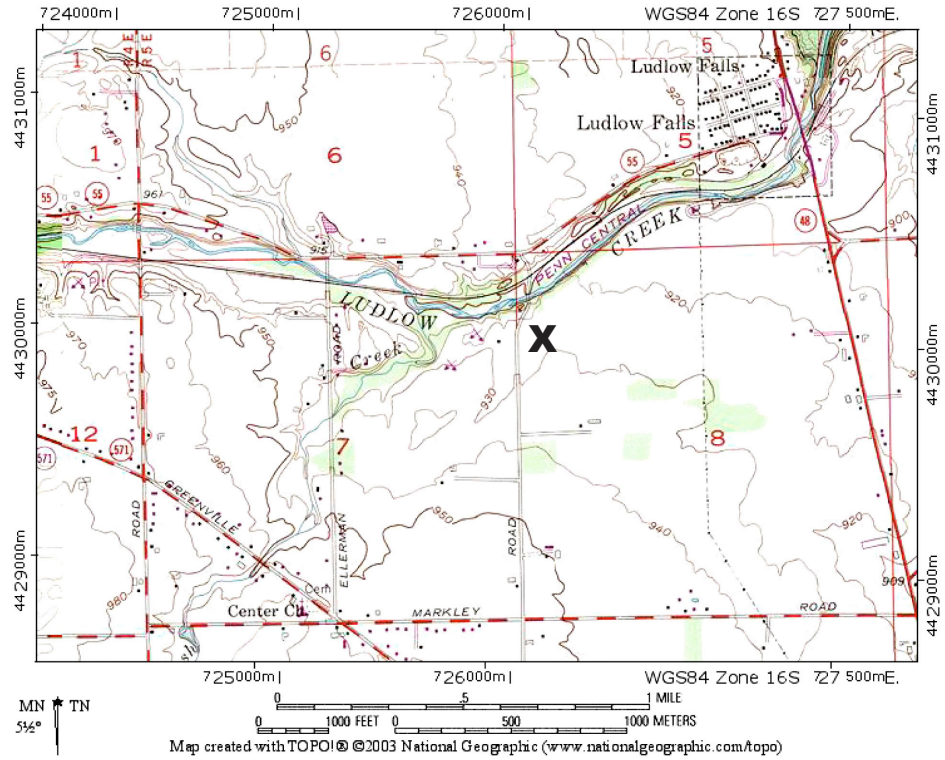


Figure 2. Location of the Barrett Paving Quarry, Ludlow Falls, Miami County, Ohio.

Figure 3. The main pit of the Barrett Paving Quarry.

silt that is high compared to subjacent and superjacent formations (Stout, 1941; Elliott, 1984). Previous studies (Collier-Malone, 2004) concluded that the depositional environment represented by the quarry at Ludlow Falls was a restricted- to open-marine platform, possibly lagoonal. Elliot (1984) further concluded "the Euphemia and Cedarville dolomites . . . are separated by the Springfield Dolomite . . . a dolomicrite or finely crystalline dolomite. At both the upper and lower contacts of the Springfield are discontinuous zones of pentamerid brachiopods in life position. It is suggested that deposition of the Springfield was the result of a minor regression which, aided by the pentamerid brachiopods banks, resulted in restricted conditions." Because much of the fauna in the Springfield Dolomite at this location is in the life position (nearly all of the trilobite specimens are prone, not enrolled), it can be assumed that the sudden influx of siliciclastic silts during the stated regression may have severely altered the water conditions, causing the death of so many specimens in one location.

Figure 4. The Springfield Dolomite, a finely-grained dolomicrite. Inset shows sample in thin section, with Alazarin red stain indicating a 5% calcite/95% dolomite composition.

Scientific Background

H. J. Harrington (in Moore, 1959) remarked that a "wholly satisfactory, natural classification of the trilobites is beyond possibility at the present moment." He cited that the fault was not with the fossils, but with the then current understanding of the "truly relevant and diagnostic" characters used for the establishment of familial and suprafamilial taxa. Harrington defined seven "roadblocks" to a natural classification. They included:

- An entire lack of knowledge concerning the internal anatomy of trilobites
- Inadequate knowledge of larval development
- Insufficient data on the ventral appendages
- Unsatisfactory knowledge of the ventral cephalic sutures in many genera
- Inadequate understanding of the original cephalic segmentation
- Homeomorphy of some of the trilobites
- Possibility that some trilobite lineages may have developed a mineralized carapace late in their phylogenetic evolution

Previous Studies – The classification of trilobites has long been a challenge, if for no other reason than the number of species involved. The Trilobita have already been organized into nine orders, with over 150 families, approximately 5,000 genera and more than 15,000 species. There are differences in body shape, exoskeletal texture, the sutures that join the exoskeleton plates, and the eyes. Systematization of the fossil record of trilobites into a scheme that reflects the phylogeny and evolution of different stocks in a consistant manner has been the constant preoccupation of paleontologists since the nineteenth century (Levi-Setti, 1993).

Since the first classification of trilobites by Brongniart (1822), many descriptions and groupings of taxa were based on morphological characters that were "having less than secondary value." (Harrington in Moore, 1959). Throughout the 19th century, there were numerous attempts to reclassify the trilobites. Dalman (1827) reclassified them into just two groups, based on wheher they

possessed eyes or not. Quenstdt (1837) proposed a classification that defined the group by the structure of the eyes and thoracic segments. Futher attempts at reclassification are summarized in Table 1.

In 1897, C. E. Beecher attempted to establish a "natural" classification based on biological features. Beecher's proposal was greatly influenced by Haeckel's famous "law of morphogenesis" – that the ontogenetic development of the individual recapitulates the phylogenetic development of the species (Harrington in Moore, 1959). Beecher reclassified trilobites into three orders, containing just 14 families. A former student of Beecher's, Percy E. Raymond, adopted Beecher's classification in his work. Raymond's (1913) contributions to the *Textbook of Palaeontology,* including the addition

Table 1. History of Reclassification During the 1800s

Year	Pioneer	Characters Used for Classification
1839	Emmrich	Ocular characters and shape of pleurae
1840	Milne Edwards	Enrollment ability
1843	Goldfuss	Based on Dalman's work The presence or abssence of eyes and structure
1843	Burmeister	Accepted Milne Edward's work Stressed size of pygidium and characters of pleurae
1845	Emmrich	Thoracic features, structure of the eyes, and facial sutures
1847	Hawle and Corda	Pygidium features
1849	M'Coy	Presence or absence of articulating facets on the pleurae
1852	Barrande	Structure of pleurae
1864	Salter	Number of thoracic segments, size of the pygidium, occular characters and facial suture characteristics
1889	Chapman	Arbitrary chracteristics
1896	Haeckel	Presence or absence of a "true" pygidium

of 14 new families, gained him world wide recognition as a pioneer in the field. Beecher's classification was not without objectors, having been criticized by no fewer than twelve fellow scientists in 16 publications up to 1959. Although modified by Swinnerton in 1915 (including some of Jaekel's ideas), Richter in 1933, and Størmer in 1942, the classification was still found to be "completely untenable."

European palaeontologists did not accept Beecher's work, and in 1907, Gürich proposed a new classification based on the number of thoracic segemnts and pygidium size. It was viewed as a combination of the work of Quenstedt, Emmerich, Burmeister, Salter, and to some extent, Beecher. In 1909, Jaekel proposed modifications that were later adopted by modern pioneers Whitehouse and Hupé. Gürich proposed two orders, comprising of four suborders – one including three groups.

C. Poulsen's (1927) reclassification of the class Trilobita – based completely on facial sutures – differed from Beecher and Swinnerton, and included an additional order. Poulsen's classification included three orders with two suborders.

Until the release of the trilobite volume of the *Treatise on Invertebrate Paleontology* in 1959, the last comprehensive discussions were by Pierre Hupé (1953, 1955) and Henningsmoen (1951). Hupé's classification followed Stubblefield's prediction that "it will probably be found that the safest criteria of affinity are collective characters developed in the axial region of the shield" (Harrington in Moore, 1959). Harrington further clarified this to mean "especially the cephalon." Henningsmoen, accepting Størmer's views on the glabellar furrows, stressed the importance of the development of the glabella and the "form, direction, and relative position of the glabellar furrows" (Harrington in Moore, 1959).

In 1997, thirty-eight years after Harrington, Fortey concluded that a "wholly satisfactory, natural classification of the trilobites is beyond possibility at the present moment" is still true. In the revised trilobite volume of the *Treatise on Invertebrate Paleontology*, Fortey (1997) recognized that of the 170 families described and classified by Hupé (1953, 1955), nearly all are accepted today. He

further clarified that the recognition of a family implies that several genera share some well-characterized features that permit their inclusion in a higher taxon. But at what point do shared characteristics define inclusion into a family, or the assignment of a new genus, or the discovery of a new species? It is this simple distinction that has caused the need for advances in phylogenetic systematics and morphometric analysis – advances necessary to correctly reclassify any group of organisms.

There have been several different approaches to the classification and phylogenetics of trilobites over the last 75 years (Fortey, 2001). During the 1970s and 1980s, the development of cladistic methods introduced a new way of examining and classifying taxa – through character-based parsimony analysis. Problems in discriminating convincing morphological characters used to define clades have led to improper family definition.

Cladistic analyses of trilobites have evolved from the pioneer efforts of Eldredge (1972, 1977), to computer-based analysis which have recently been used to completely reclassify various families. Fortey and Chatterton (1988) and Fortey (1990) approached classification from the viewpoint of phylogenetic systematics, using axial, ventral, larval, and sutural characters in particular (Fortey, 2001). Large scale synapomorphies were sought in order to define natural groups within a selected range of family-level taxa. Fortey (2001) wrote "Phylogenetic analysis of accepted families has started but there is plenty of opportunity for further studies, using techniques which are now standard. There is no substitute for careful morphological descriptions based on a basis for such analysis… ."

Formal descriptions of calymenid trilobites began in the 1820s. Brongniart first defined *Calymene* in 1822. This was followed by Shirley (1936) defining *Gravicalymene* and *Flexicalymene*, Siveter (1977) describing *Sthenarocalymene* and other papers. In 1980, Chatterton and Campbell described another genus, *Apocalymene*, all without the use of parsimony and morphometric analysis. Raymond (1916) described *"Calymene" celebra* and placed it within *Calymene* based upon characters he thought important. Others have since then reassigned it.

Classification of Species

> "The first step in wisdom is to know the things themselves; this notion consists in having the true idea of the object; objects are distinguished and known by their methodical classification and appropriate naming; therefore, Classification and Naming will be the foundation of our Science"
>
> –LINNAEUS (1735), QUOTED IN STEVENS (1994:201)

Until early in the nineteeth century, the dominant idea of the natural order was that of a *scala naturae*, an unbroken sequence from the most primitive to the most advanced organisms (Panchen, 1992). It was in the 10th edition of *Systema Naturae* in 1758 that Linnaeus first proposed the classification of *Regnum* (Kingdom), *Classis*, *Ordo*, *Genus*, and *Species* (to which phylum and family were later added) – that "all taxa at the same level in the hierarchy occupy the same rank and are given the same catagory" (Panchen, 1992). Linnaeus believed in an inclusive hierarchy that was divergent, where a taxon of a specific rank belongs to only one taxon of higher rank (genus or above); and irregular, in which the whole would not be expected to have a fixed symetrical pattern.

A number of naturalists revolted against the acceptance of *scala naturae* early in the nineteenth century, stating that organisms – specifically animals – could not possibly be arranged naturally in a linear order. One such scientist, Baron Cuvier, proposed that there was no "organizing principle of scala, that the characters by which animals are classified are all adaptive" (Panchen, 1992). Cuvier recognized that characters can be arranged by adaptive importance and stability, therefore defining a hierarchy of ranks. In his 1827 *The Animal Kingdom Arranged in Conformity with its Organisation*, he wrote: "The separate parts of every being must…possess a mutual adaptation; they are therefore, certain peculiarities of conformation which exclude others, and some again which necessitate the existence of others. When we know any given peculiarities to exist in a particular being we may calculate what we can and what we cannot exist in conjunction with them.

The most obvious, marked and predominant of these, those which exercise the greatest influence over the totality of such being, are denominated its important or leading characters; others of minor considerations are termed subordinate." From Cuvier's principles arose the classification of the animal kingdom, characterized by four "embranchments," each a separate adapted creation within the kingdom. Each branch was divided into four classes, which were then further subdivided.

In his *Essay on Classification* in 1857, Louis Agassiz adopted Cuvier's work and published his taxonomic hierarchy based on body plan. The obvious flaw to Agassiz's work was that he was a "progressionist" and therefore, rejected evolution. His taxonomic tree recognized that not only was each species a real entity, but so was every taxonomic category.

Throughout the nineteenth century, the debate raged on over the natural order of beings, and whether classification could follow *scala naturae*. The German school of *Naturphilosophie*, led by Oken, and the French transcendental morphologists led by Siant-Hiliare, speculated about a parrallel between ontogeny and the *scala naturae*. It was the work of Karl Ernst von Baer, refuting the *scala naturae* interpretation of ontogeny, that established the principle of divergence – the accumulation of different physical characteristics between groups that can lead to the formation of new species, often the result of different groups of the same species adapting to different environments, leading to mutations. It can be seen in some higher-level characters of structure and function that are readily observable in organisms. Von Baer saw taxonomic characters as a nested set of "*Baupläne*" (fundamental body plans) within each embranchment (Gould, 1977).

Prior to the 20th century, the use of evolutionary history as a basis of classification was unheard of. It wasn't until Charles Darwin published his theory of evolution through natural selection, which included the idea of common descent, that the very concept of phylogeny – an organism's evolutionary history – arose. Because it is thought today that ideally classification should reflect evolutionary relationships, taxonomists have adapted the Linnaean system to better represent evolutionary relationships.

The idea of the genus as the smallest "kind" of plant or animal that can be recognized without close study was an extremely important one in the earlier periods of taxonomy (Bartlett, 1940). In 1953, Just affirmed that "from a purely systematic point of view, the genus still comprises the most effective taxonomic unit on which new classifications of higher groups can be based . . . ." In contrast, Linneaeus' attitude towards the species was much more modern. Linneaeus thought that "the species could be regarded with confidence as a morphologically stable group of individuals. . ." (Svensen, 1945).

> "The species was a subdivision of it [genus], often requiring expert examination both before it could be named, since the specific name was at once a qualification of the generic name and a differentiation from all other specific names within that genus" (Cain, 1956).

Linnaeus found it necessary to consider species as separate entities, while naming them as parts of genera. While the scientific community has embraced Linneaeus' hierarchy of kingdom, phylum, class, order, family, genus, and species, several problems have arisen; first, "there is no reason to suppose all (natural) genera will be found to have well-marked attributes both common to and peculiar to all their members" (Cain, 1956). Second, because there is no law governing and quantifying the angles of divergence of different stocks branching from the same evolutionary line, it would impossible to speculate that all genera are clearly discrete at any one time (Cain, 1956). This is further confused by the discoveries of new isolated species that represent forms halfway between two genera, but are equally included in both or neither.

As Darwin had theorized, the world's species seem to naturally arrange themselves into groups that are subordinate to groups based on their similarities and differences. Before Darwin recognized such a pattern, scientists attributed such regularity to God or to other universal ordering principles. Because his theories explained the hierarchical pattern of resemblance – species in a

common genus are similar because they evolved from a common ancestral species, the founder of that genus – Darwin's ideas gained instant appeal.

For the purposes of this study, a species is defined phyogenetically as "a single lineage of an ancestor-descendent population that maintains its identity from other such lineages and has its own evolutionary tendencies and historical fate (Simpson, 1961; Wiley 1978, 1981). This is known as the Phylogenetic Species Concept.

Because most classifications are based upon readily observable characteristics, either appearance, behavior, or geographic or stratigraphic occurence, species constituting the genera of a common family still look somewhat alike because they share an even earlier antecedent. But it's not that simple: *overall similarity* is an unreliable guide to genealogical relationship because different lineages evolve at different rates. The need to distinguish these two kinds of traits (derived versus ancestral) in establishing genealogies is one of the essential contributions of the German entomologist Willi Hennig (1913-76), the founder of modern-day cladistical analysis – understanding evolutionary trends by comparing a specific set of derived characteristics from each specimen with one another, and then classifying the organisms based upon these trends.

If this classification is to accurately reflect phylogeny, we must be able to assess the genetic difference between species. Since genetic difference cannot be observed directly in fossils, the use of morphological difference as a rough measure of genetic difference is used. The two species in a group that have the largest number of morphological characters in common are most likely to be descended from a common ancestor and thus are most likely to qualify as members of a single higher taxon (Raup and Stanley, 1978).

Diversity of Trilobita in the mid-Silurian of Southwest Ohio

During recent studies on the depositional history and environments of the mid-Silurian limestone and dolomite quarries of southwestern Ohio, it was discovered that the diversity of the trilobite fauna previously described was inadequate. However, it is not the number of different species that stands out in these quarries, but the shear numbers of specimens. It is at the Barrett Paving Quarry in Ludlow Falls, Ohio that this phenomena is greatest.

Specimens from four different orders are represented: Phacopida, Lichida, Coryexochida, and Odontopleurida. Within the order Phacopida, three species of *Dalmanites*, two species of *Encrinurus*, and one species in each genus of *Calymenidae*, *Deiphon*, *Staurocephala*, *Sphaeroxochus*, and *Trimeris* have been identified. Within the order Lichida, a single species of *Arctinurus* and *Metropolichas* have been identified, as well as multiple species of *Bumastus* within the order Coryexochida, and a single species of *Dudleyaspis* within the order Odontopleurida (see Figures 5 and 6).

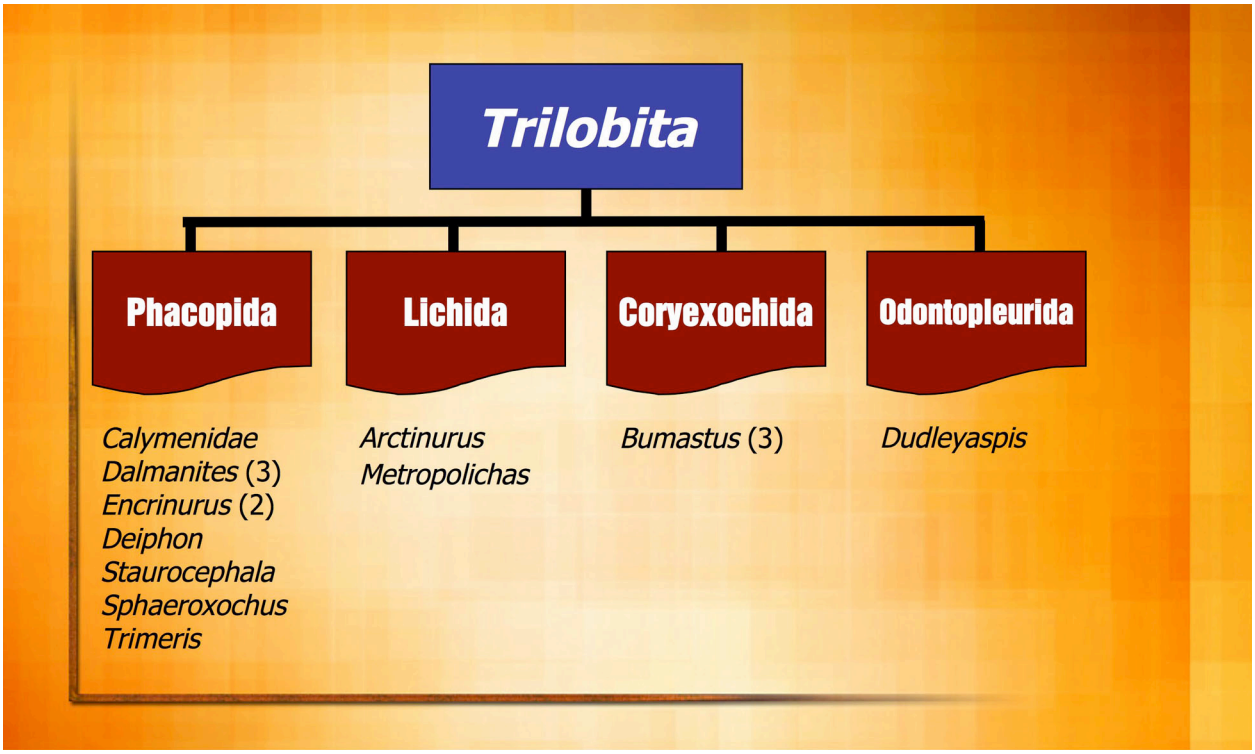


Figure 5. Trilobite diversity in the southwestern Ohio quarries.

Arctinurus

Bumastus

Bumastus

Calymene

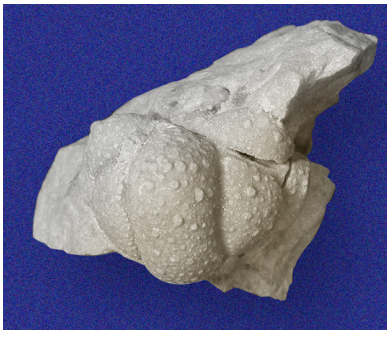
Dalmanites

Dalmanites

Dalmanites

Deiphon

Encrinurus



Sphaeroxochus

Dudleyaspis

Figure 6. Examples of trilobites from The Barret Paving Quarry

However, more than 98% of the specimens come from a single species within the family Calymenidae. While trying to identify these specimens, an interesting problem was discovered. The species first described as *Calymene celebra* has been assigned to five genera in the past 100 years.

Raymond (1916) described *Calymene celebra* from Silurian strata of southeastern Wisconsin. Shirley (1936) defined two new calymenid genera, *Gravicalymene* and *Flexicalymene*, based on papillate lobes, and characteristics of the glabella, the preglabellar field, and anterior border. Although *"Calymene" celebra* does not have 2p papillate lobes and a fixed buttress, Shirley (1936) felt that *"Calymene" celebra* was one of the "rare occurances" of *Calymene* without this feature – another was *C. baylei*, which Shirley (1936) left assigned as *Metacalymene* by Kegel (1927). Whittington (1971) formally placed *"Calymene" celebra* within *Flexicalymene,* and then later (1992) informally referred to it as *Gravicalymene*. Siveter described *Sthenarocalymene* in 1977 without reassigning *"Calymene" celebra*. Chatterton and Campbell (1980) reassigned *"Calymene" celebra* to *Apocalymene*, although Holloway (1980) felt *Apocalymene* was synonymous with *Sthenarocalymene*, leading to *"Calymene" celebra* being informally reassigned to *Sthenarocalymene*.

What compounds the confusion is that the characters used to seperate the genera within the family Calymenidae, and therefore create the basis for the argument to create a new genus, seem weak at best. Coupled with the use of incomplete specimens in descriptions of new genera, overinflation of genera is not only possible, but a reality. In the absence of DNA, the question becomes whether these differences in morphological characteristics are significant enough to warrant a new genus, or simply enough to warrant a new species. There are many cases in which morphological differences within species are extreme – take a toy poodle and bull mastiff for instance. It is purely conceivable that many of these "new" genera may be the result of interbreeding, accounting for the slight variations in morphology. It has long been accepted that "hybrids were to be recognized as such, but if they achieved relative constancy, then they merited the status of species" (Cain, 1956).

State of the Family Calymenidae

> "The trilobite *Calymene blumenbachii* from the Silurian at Dudley, England, had a fundamental role in the early study of this prominent group of extinct arthropods. Discovered during the mid-1700s, this was the first trilobite known from numerous complete and well-preserved fossils anywhere in the world."
>
> Mikulic and Kluessendorf, 2007

The discovery of *Calymene blumenbachii* (the Dudley locust) in 1749 by Charles Lyttleton, and its subsequent inclusion within the family Calymenidae in 1843 marked the legitimate beginning of trilobite research. In *Legacy of the Locust – Dudley and Its Famous Trilobite*, Mikulic and Kluessendorf (2007) state that Lyttleton submitted a letter to the Royal Society of London in 1750 concerning a "petrified insect" he found in the "limestone pits at Dudley" (see Figures 7, 8).

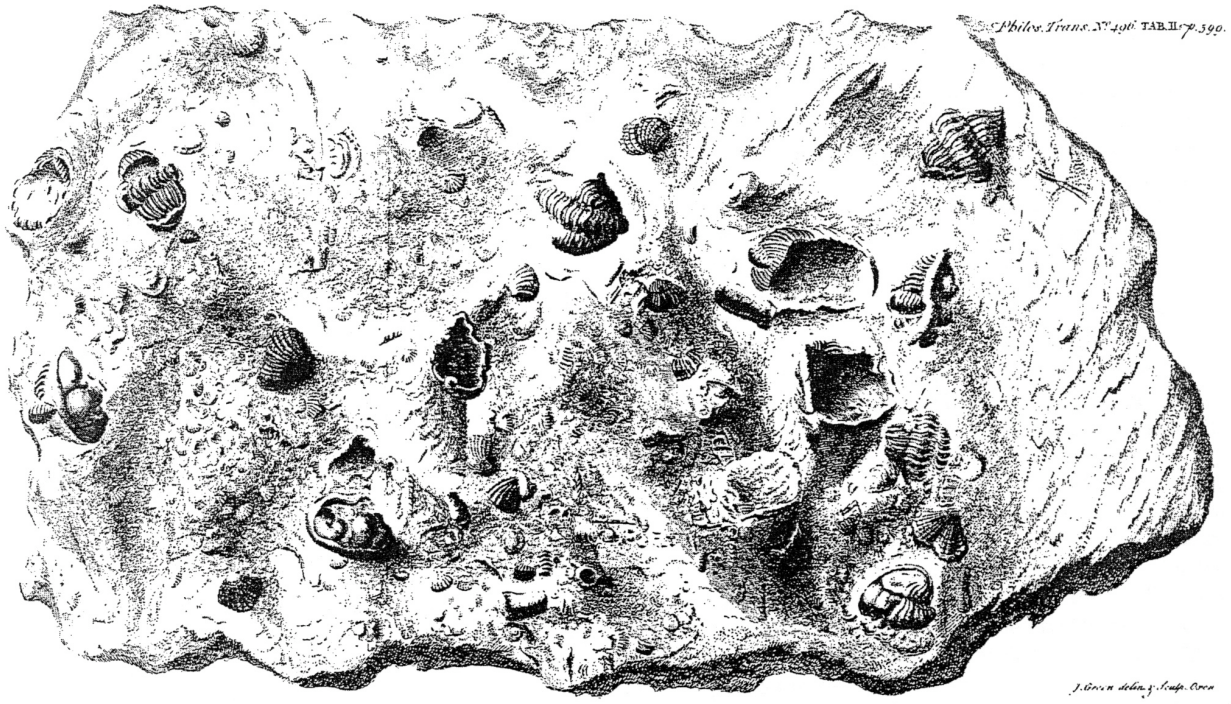


Figure 7. A slab of limestone from Dudley, England, with embedded *Calymene* trilobites (Table II, Lyttleton, 1752; Mortimer, 1752)

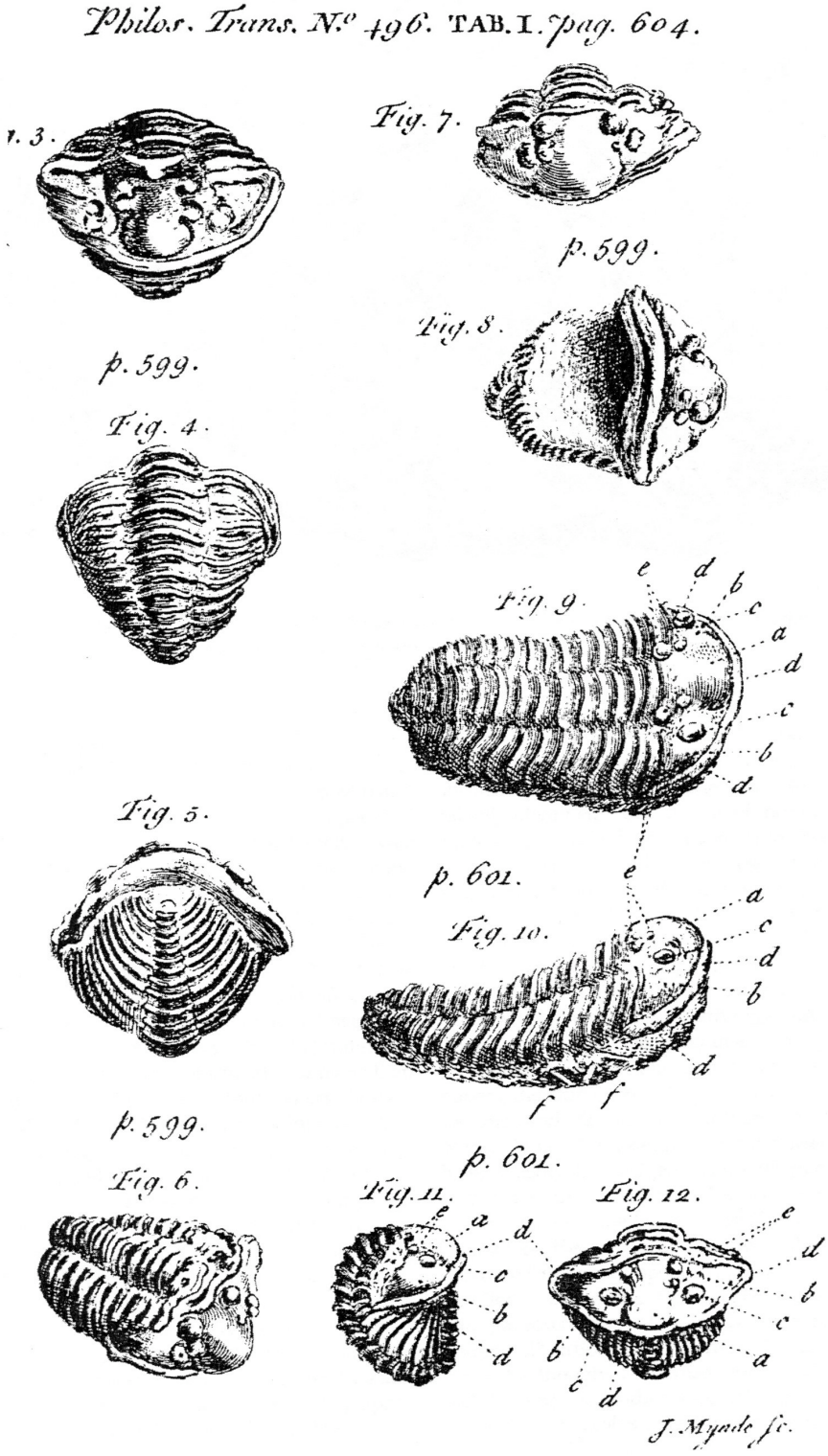


Figure 8. Earliest known illustrations of the Dudley fossil (Table I, Lyttleton, 1752; Mortimer, 1752)

In 1754, Manuel Mendez da Costa responded to the Lyttleton and Mortimer papers, proclaiming that the Dudley locust was not an insect, but instead belonged to "the crustaceous tribe of animals." He proposed that the Dudley specimens should be called *Pediculus marinus major trilobos*, a name which lasted well into the 1800's.

German naturalist Johann Walch initiated the first inclusive study of this group including an examination of all previous literature, and a hands-on study of many of the collections in Europe. Within his published results, he proposed the use of the name "trilobite" for this group of organisms. He chose this name because he thought it was more appropriate to name them after their unique three-lobed character then their supposed analogous living relatives or the localities at which they are found, as had been common previously (Mikulic and Kluessendorf, 2007).

Authors well into the nineteenth century included the Dudley fossils in a variety of general natural history books and other publications, serving as the only trilobite mentioned, and being representative for the entire group. Another German naturalist – Johann Friedrich Blumenbach – listed the Dudley fossils in his *Handbuch der Naturgeschichte*. It is thought that Blumenbach's work on the Dudley fossils inspired the French scientist Alexandre Brongniart to formally name it *Calymene blumenbachii* (see Figure 9) in his honor. Brongniart's paper (Brongniart, 1822; see also Desmarest, 1816, 1817), like that of Walch's, is considered to be one of the most influencial trilobite

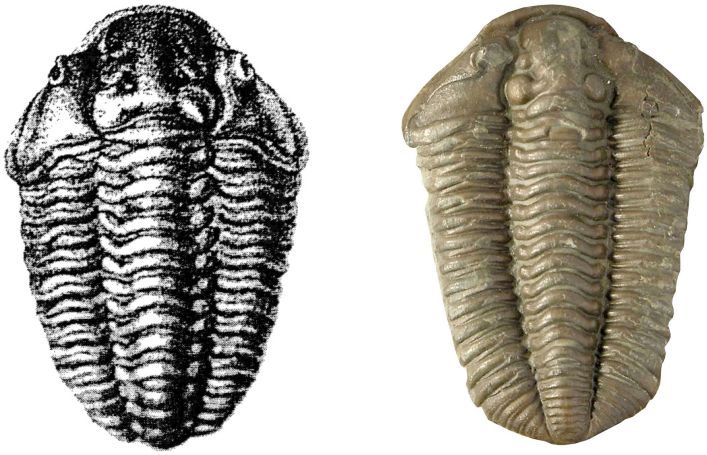


Figure 9. *Calymene blumenbachii* (left, illustration from Brongniart, 1822; right, actual specimen)

studies of the 1800's. Walch may have established the arthropod affinities of trilobites, but Brongniart's paper marked the beginning of modern trilobite classification.

Expanding on the work of Brongniart and others, German zoologist Herman Burmeister (1843) published a comprehensive examination of trilobites which he proposed a high-level classification of the group. One of his new families, the Calymenidae – which represented, in part, "trilobites having the power of rolling themselves into a ball . . ." – was based on *Calymene blumenbachii* specimens (this family is now credited to Milne Edwards (1840), who proposed a similar family name for a group with many of the same trilobite taxa.)

In 1864, Salter established the order Phacopida, placing the family Calymenidae within it. The official taxonomic lineage of the calymenid trilobites according to the *Treatise on Invertebrate Paleotology* (1959) is as follows:

- **Order PHACOPIDA Salter,** 1864
  [*nom. transl.* HARRINGTON & LEANZA, 1957, *ex* Phacopini SALTER, 1864]
  [=order Proparia BEECHER, 1897; order Phacopida HARRINGTON & LEANZA, 1957 (erroneously attributed by Thorn to RICHTER, 1932)] [Type-*Phacops* EMMRICH, 1839]

  An order of post-Cambrian trilobites, probably derived from the Ptychoparida. Cephalon with facial sutures typically proparian (most Phacopina and Cheirurina) or gonatoparian (most Calymenina, some Cheirurina), but may be opisthoparian (some Calymenina and Cheirurina) or even lacking (some Cheirurina); glabella variously shaped, commonly expanding forward (Phacopina, most Cheirurina) or tapering forward (Calymenina, some Cheirurina), lateral glabellar furrows (if present) variously developed; preglabellar field short (sag.) or lacking; rostral plate present (Calymenina, most Cheirurina) or lacking (Phacopina, some Cheirurina). Thorax with 8 to 19 segments. Pygidium mostly medium to large, but small in some exceptional early representatives. *L.Ord.-UDev*.

- **Suborder CALYMENIA Swinnerton,** 1915
  [=Superfamily Calymenidea RUD. RICHTER, 1933; superfamily Calymenacea KOBAYASHI, 1935; superfamily Calymenoidae HUPE, 1953 (attributed to SWINNERTON, 1915)] [Type-*Calymene* BRONGNIART, 18221

  Exoskeleton medium to large in size. Cephalon semicircular to subtriangular, with or without border. Glabella narrowing forward, bell-shaped to trapezoidal in outline, with four

or fewer pairs of lateral furrows of varying depth (in a few forms no furrows); posterior adaxial parts of fixigenae commonly differentiated as distinct quartercircle-shaped tracts (paraglabellar areas); genal spines mostly lacking (present only in a few Ordovician genera); posterior sections of facial sutures cutting margins of cephalon mostly at or in front of genal angles. Hypostoma subrectangular, small anterior wings with indented posterior margin (except in a few early forms with rounded margin). Thorax narrowing moderately backward; almost uniformly composed of 13 segments but rarely with fewer; axis occupying 0.3 or more of thoracic width; pleural ends rounded. Pygidium transversely elliptical to elongate triangular, mostly medium to large (small in early genera only), with number of segments ranging from few in early genera to many in later genera; pleural portions downward-backward from axis. *L. Ord.-M.Dev.*

Opinions differ as to whether trilobites assigned to the Calymenina are opisthoparian. In this connection, it is pertinent to note that (1) affinities of the Calymenina (especially early forms) to ptychopariid trilobites are far greater than with any other trilobite group, and (2) some Calymenina (e.g. Pharostoma, Pharostomina, Bavarilla) possess genuine librigenal spines, whereas no genus of the assemblage incontestably bears hxigenal spines in the adult. Two fairly homogeneous evolutionary lines can be recognized in the Calymenina, which respectively are grouped in the families Calymenidae and Homalonotidae. They must have split apart early in Ordovician time or before. The Homalonotidae may have been derived from the early Tremadocian genus Bavarilla or a similar form. The Calymenidae may be descendants of the early Tremadocian Pharostomina, or alternatively, may have branched off from the homalonotid stem somewhat later in Ordovician time through Synhomalonotus. The first possibility seems to be more probable.

- **Family CALYMENIDAE Burmeister,** 1843

  [=Calymmenidae ANGELlN, 1854]

  Cephalon semicircular, convex, glabella bell-shaped or parabolic, widest across occipital ring or preoccipital lateral may or may not project in front of genae, with 2 to 4 pairs of lateral furrows; lateral lobes of glabella diminishing in size forward, tending to be isolated by shallow furrows from median lobe and independently convex, 2nd *(2p)* and 3rd *(3p)* lateral lobes (counting forward) may be papillate (that is, with distal edge in contact with projection from gena on opposite side of axial furrow); axial furrows bordering lateral glabellar lobes deep, anterior pit deep; genae highest adjacent to axial furrows, sloping

steeply downward anterolaterally; relatively small eye lobes situated on highest part of genae opposite *2p* or *3p* glabellar lobes; low eye ridges may be present; convex anterior, lateral, and posterior cephalic borders clearly defined by broad furrows, which become shallow or die out close to facial sutures; doublure rolled under borders and not extending inside them; frontal area variable in length *(sag.)*, in some forms extending into frontal spine; preglabellar furrow and anterior border variable in form; anterior sections of facial sutures running directly forward from eyes and then curving inward to cross border outside projected line of axial furrows. Rostral suture transverse on doublure in some genera, connective sutures converging backward; rostral plate widest at anterior margin and sharply flexed upward under border; posterior sections of sutures running backward-outward in anterolaterally convex curve to cross border at rounded genal angles which may bear short spine or tubercle on posterior edge inside of suture lines. In *Pharostoma* (and *?Bathycheilus*) sutures cut posterior margins just inside relatively long genal spines. Hypostoma longer than wide, subovate middle body divided by short, shallow, diagonal middle furrows so that posterior lobe is crescentic; macula faint, smooth; anterior lobe may have raised central portion; exoskeleton at anterior border flexed so that edge faces ventrally, hypostoma with large anterior wing bearing prominent wing process, posterior wing small; wide lateral notch, behind which lateral and posterior borders are wide, with deep median notch adjoining parts of border drawn out into blunt points. Thorax with ?11, 12, or 13 segments; axis convex; pleurae bent downward at fulcrum and almost vertical distally; axial rings undivided, but distal portion swollen; deep articulating furrows and apodemal pits, inner part of pleurae horizontal, with deep slightly diagonal pleural furrow, outer part with wide facet partly indented by pleural furrow; articulating processes and sockets in axial furrows and at fulcra; narrow doublure around outer part of pleurae, projecting inward at anterior edges. Pygidium with axis extending almost to posterior margin, sloping steeply backward and sideward; anterior edge of pleural fields curving back, maximum width between anterolateral corners; axis divided by 5 to 8 ring furrows that are deepest abaxially, posterior tip of axis unfurrowed; pleural fields un furrowed or with deep pleural furrows and shallow interpleural grooves; mostly without border; pygidial doublure narrow and rolled tightly under margins. External surface commonly granulose, tuberculate, or both, with deeper parts of furrows smooth. Fine canals penetrating exoskeleton scattered over surface, largest on anterior border of cephalon and posterior part of pygidium, smaller in tubercles along axis. *L. Ord.(Arenig.)-M Dev.*

The addition of new genera progressed slowly throughout the remainder of the nineteenth century and well into the 1900s. The genera *Neseurtus* was added by Hicks (1873) and *Calymenella* by Bergeron (1890). Up until this point, all work on the family Calymenidae was of European in origin. It wasn't until 26 years later that *Hemicrypturus clintonii* Vanuxem from the Clinton Group (Silurian) of New York, was reassigned by American paleontologist Percy Raymond to *Liocalymene*. This began a series of reclassifications that continues to this day. In 1918, Novak reassigned *Calymene (Synhomalonotus) arago* to *Colpocoryphe*, and Kegel (1927) reaasigned *Calymene baylei* Barrande to *Metacalymene*.

In the same publication that Raymond reassigned *Liocalymene*, he described two new species of Calymenidae. The first was *Calymene breviceps* from the Waldron Shale in Indiana:

> CALYMENE BREVICEPS, "Calymene" nov.
> (see Figure 10)
>
> The Calymene abundant at Waldron, Indiana, has always been identified with *C. niagarensis*, but differs from that species in at least two marked details. The first and most obvious characteristic is that there is no lip, nor any furrow between the glabella and the rim, so that the glabella reaches upon, and in some cases, overhangs the rim, a feature usual in the Cheiruridae but extremely uncommon among (the Calymenidae. This gives the cephalon the high, short appearance which suggested the name breviceps. On the pygidium the ribs reach nearly to the margin but become faint on approaching it. Ordinarily the ribs do not bear any median impressed line though traces of one may be seen on some specimens.
>
> This species is in many ways much like *C. celebra*.
>
> *Formation and locality:* – Currently, this species is known only from the (Silurian) Waldron shale at Waldron, Indiana, where it is very common.

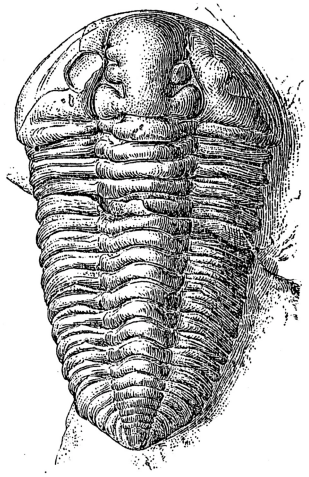


Figure 10. *Calymene breviceps Raymond.* An entire specimen from the Waldron Shale (Silurian), Waldron, Indiana. Holotype (Museum of Comparitive Zoology, 640).

The other species that Raymond (1916) referred to and described was *Calymene celebra*, from Silurian deposits at Grafton, Illinois.

CALYMENE CELEBRA, sp. nov.
(see Figures 11 & 12)

Calymene blumenbachii var. *niagarensis* Hall, Geol. surv. Wisc., 1862, 1, p. 432.

Calymene niagarensis Hall, 18th Rept. N. Y. state cab. nat. hist., 1865, p. 30, adv. sheets; 20th Rept. N. Y. state cab. nat. hist., 1868, p. 334; 1870, rev. ed., p. 425. Weller, Bull. Chicago acado scL, no. 4, pt. 2, p. 261, pI. 23, f. 9-10.

One of the most abundant of the trilobites of the Chicago area and of southeastern Wisconsin is a Calymene which is constantly identified as *C. niagarensis*. It is quite commonly found entire, but always (so far as the author has seen) in the condition of a cast of the interior. Moulds of the exterior are common, but seldom complete.

The cephalon is like that of *C. niagarensis*, with a short lip, and narrow furrow in front of the glabella. The dorsal furrows are always very deep and sharp, but this is due to the state of preservation. The

glabella tapers rather abruptly toward the front. The basal lobes are large, rounded, almost isolated; the second lobes small and rounded, the intermediate "extra lobes" not very prominent. The third lobes are very small and the fourth ones just barely indicated. The frontal lobe is short and rather square at the front. The eyes are close to the glabella and opposite the furrows between the second and third pairs of lobes.

The pygidium is the most characteristic portion of the animal. The axial lobe is narrow, well defined, and has rings. The pleural lobes show four pairs of narrow ribs, without impressed line, which reach only halfway to the margin. The fourth of the four pairs are very faint and short. Each pleural lobe is thus divided into a small triangular ribbed portion near the axial lobe and a much longer smooth portion below. This pygidium presents the greatest possible contrast to *C. niagarensis*, in which the ribs are more conspicuous near the margin than near the axial lobe. The peculiarities of the pygidium have doubtless been noticed before, and probably have been explained as due to the state of preservation, the specimens all being internal casts. Internal casts of either cephala or pygidia of trilobites are practically always less and not more smooth than the exteriors, however, and cleaned interiors of *C. senaria, C. breviceps,* and *C. meeki,* all show that Calymene follows the general rule. *Calymene celebra* shows a halfway stage to what is achieved in *C. clintoni* Vanuxem, namely, a pygidium with smooth pleural lobes. The latter species is too far removed from the Calymenes with typical ribbed pygidia to be included in the same genus.

Formation and locality: – Calymene celebra is common in the Niagaran of the Chicago district in northern Illinois, in the same portion of the Silurian in southeastern Wisconsin, and also near Madison, Indiana, and Eaton, Ohio.

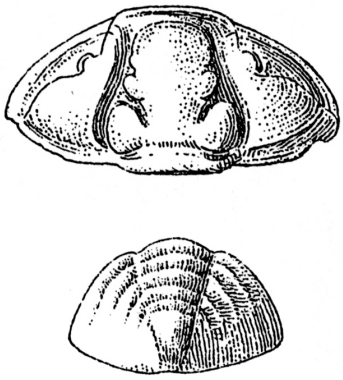


Figure 11. *Calymene celebra* Raymond from the Silurian dolostones of Grafton, Illinois. The cephalon of one entire specimen and the pygidium of another, the two specimens being the syntypes of the species (MCZ 638, 639).

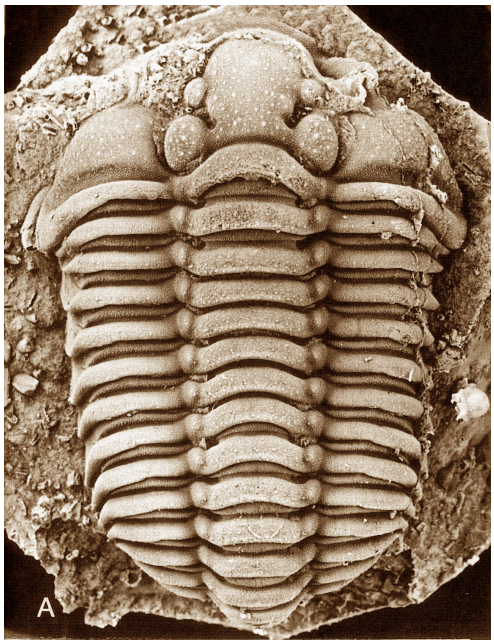


Figure 12. A photograph of *Calymene celebra* Raymond.

However, the most complete early reclassification of *Calymene* came from Shirley (1936). Shirley noted that many new species had been described up to that point in time, especially in America and almost without any mention of their relationship with respect to the work of Pompeckj (1898), who separated the genus *Synhomalonotus*. He regarded the "subgenera" *Calyemene* (restricted), *Pharostoma*, *Synhomalonotus*, and *Ptychornetopus* as independent genera.

Shirley (1936) described this first attempt to reclassify *Calymene*, and its shortcomings: "Pompeckj further divided the species of "*Calymene*" into three series. In the first series – *C. senaria* Conrad thru *C. platyi* Green, including the genotype *C. blumenbachii* Brongniart – he believed that there was a passage between the senaria-like forms and the Silurian forms grouped around *C. blumenbachii*. Although Pompeckj noticed, as an important character, the narrowing (due to a buttress on the fixed cheeks) of the axial furrows in the Silurian forms, it will be shown that there were no known transitions. The series is therefore heterogenous and cannot be maintained.

"The second series, *C. cambrensis* Salter thru *C. declinata* Barrande, was founded upon a combination of many characters. These characters can be shown to be evolutionary: that is, they mark stages in development only, or are absent from the types of the species which were placed within the group. For example, Pompeckj says that an important character is the strong forward projection of the preglabellar field. Whether the preglabellar field projects forward or not depends upon its attitude relative to the glabella, and this can be shown to change gradually. Another character said to be possessed by members of this series is an intermediate lobe between the first (posterior) and second glabellar lobes. The type specimens of *C. cambrensis* and *C. brevicapitata* Portlock are entirely without intermediate lobes, *C. caractaci* Salter has very slight intermediate lobes, and specimens of *C. declinata* show no sign of them. Pompeckj's second series cannot, therefore, be maintained.

"His third series included *C. foveolata* Törnquist and *C. leptoenarum* Törnquist, shown by Schmidt and Warburg (1925, p. 155) to belong to *Pharostoma*, *C. callicephala* Green, of which the holotype is now lost (Bassler, 1915, vol. 1, p. 166), *C. mammilata* Hall, *C. tuberculosa* Salter (= *C. nodulosa* Shirley), and *C. stacyi* Schmidt (pars). The last three species are certainly unrelated to one another. Pompeckj's third series, therefore, also falls."

Shirley (1936) went on to recognize that since the apperance of Pompeckj's (1898) work, paleontologists had been concerned mainly with the erection of new species. However, in the years

leading up to his study, there had been attempts to subdivide the "already unwieldy" genus *Calymene* by the proposal of new genera. It was Shirley (1936) who first wrote of the need to distinguish those characters which were likely to best provide a proper basis for a new genus classification, before any importance could be given to the usefulness of the new genera.

Shirley (1936) stated, "These characters should be considered in two series. First, those relatively static and common to many members of a group and, second, those which are evolving relatively quickly and generally form the basis of the foundation of species. The characters in the first group have been called differential; those in the second group, evolutionary. It becomes necessary then to attempt a division of the characters of the species of *Calymene* into these two sets. The division cannot be sharp, but it will at least show which characters are of "group" value and can be used for the establishment of genera."

Shirley (1936) found that both the thorax and the pygidium were the most conservative parts of the calymenid exoskeleton. He wrote "The characters of the pygidium . . . are not considered to be a reliable basis for subdivision, and the variations of the cephalon must be used." He centered his research around the shape of the cephalon and glabella, differences in the glabellar lobes (including if they are papillate and in contact with the buttresses), the characteristics of the preglabellar field, and to a lessor extent, the location of the eyes.

Based on his observations and evaluation, Shirley (1936) defined and divided the Calymenidae into two groups, the first including those without development of papillate lobes, and second, those whose lobes are papillate and come into contact with the fixed cheeks. He then further subdivided the two groups based on the characteristics of the preglabellar field and the eye location.

Based on his arguments, Shirley (1936) defined as divided Calymenidae as follows:

CALYMENIDAE, H. Milne Edwards, 1840

Trilobita with gonatoparian, exceptionally proparian, facial suture; outline entire with the rare exception of small genal spines on the fixed cheeks; glabellar furrows always distinct with a tendency in all but the most primitive species to cut off the lobes from the central part of the glabella; thorax with 13, exceptionally 12, segments.

Synhomalonotus Pompeckj, 1898

Thorax with 13 segments; glabella outline sub-parabolic, truncate in front with three pairs of lateral lobes of characteristic shape and three pairs of undivid~d furrows, the first having a slight turn forward near the centre of the glabella; large preglabellar field occupied by a dome or boss.

Genotype – S. tristani (Brongniart), 1822.

Distribution – Arenig, ?Llandeilo.

The following genera have, until recently, been included in the genus *"Calymene"* in the sense of Pompeckj, 1898.

GROUP A: Without papillate glabellar lobes or buttresses on the fixed cheeks.

Flexicalymene, gen. nov.

Thorax with 13, rarely 12, segments; glabella outline subparabolic to bell-shaped; preglabellar field stretched forwards or recurved, without subsidiary ridging; axial furrows slightly contracted at each glabellar furrow.

Genotype – Calymene caractaci Salter, 1865.

Distribution – Llandeilo to Silurian.

Reacalymene, gen. nov.

Thorax with 13 segments; glabella outline sub-parabolic; preglabellar field ridged; axial furrows slightly contracted at each glabellar furrow.

Genotype – R. limba "Calymene" nov

Distribution – Lower and ?Upper Bala

Gravicalymene, gen. nov

Thorax unknown; glabella outline bell-shaped; preglabellar field recurved with roll-like edge; axial furrows slightly contracted at each glabellar groove.

Genotype and only known species – *G. convolva* sp. nov.

Distribution – Upper Bala

Metacalymene Kegel, 1927, emend.

Thorax with 13 segments; depressed form; glabella outline parabolic, truncate in front with four pairs of lateral lobes; preglabellar field relatively short, not recurved and without ridge or raised rim; faint eye-lines on the fixed cheeks.

Genotype – Calymene baylei Barrande, 1852

Distribution – Silurian (?Lower Ludlow)

Platycalymene gen. nov

Similar to *Metacalymene* but with roll-like border preglabellar field and three lateral glabellar lobes.

Genotype – Calymene duplicata (Murchison), 1839

Distribution – Llanvirn, Llandeilo, Lower Bala

GROUP B: With papillate glabellar lobes and corresponding buttresses on the fixed cheeks.

Calymene sensu stricto Brongniart, 1822

Thorax with 13, rarely 12, segments; glabella outline bell-shaped; preglabellar field recurved and without subsidiary ridge; second lobes papillate.

Genotype – C. blumenbachi Brongniart, 1822

Distribution – Silurian to Middle Devonian

Diacalymene Kegel, 1927, emend.

Thorax with 13 segments; glabella outline bell-shaped; preglabellar field recurved with strong subsidiary ridge; second lobes papillate.

Genotype – Calymene diademata Barrande, 1852

Distribution – Upper Bala, Silurian

Papillicalymene gen. nov

Thorax with 13 segments; glabella with second, third, and frontal lobes papillate with corresponding buttresses on the fixed cheeks; preglabellar field recurved without subsidiary ridge.

Genotype – Calymene papillata Lindstrom, 1885

Distribution – Silurian

Need for Reclassification – It is apparent from the abridged descriptions that there is little difference between many of these genera. In many, the cephalic7 shape is identical, only to be separated by characteristics of the preglabellar field. In particular, the differences between *Flexicalymene* and *Gravicalymene* are vague at best. *Gravicalymene* was described using only a partial cranidium (see Figure 13).

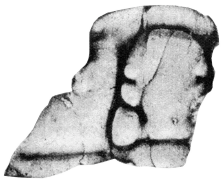
Figure 13. *Gravicalymene convolva* Shirley, 1936: plasticine impression of external mould of cranidium of holotype.

Since Shirley's (1936) work, the family Calymenidae has grown to include 33 genra. While some exhibit distinct morphological differences warranting generic status – such as *Spathacalymene* with its spatulate anterior border, many were described and assigned using minimal characteristic differences.

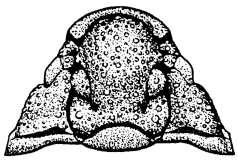
As of today, the 33 accepted genera (Jell and Adrian, 2003) are shown below (see Table 2):

Table 2. Genera and name-bearing species of the type species of genera assigned to the family Calymenidae.

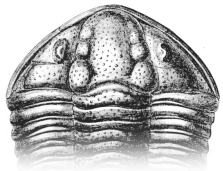
- **Alcymene** – RAMSKOLD et al., 1994 (*Calymene neointermedia* RICHTER and RICHTER, 1954) from the Hemse Formation, Gotland, Sweden; Silurian.



- **Apocalymene** – CHATTERTON and CAMPBELL, 1980 (*coppinsensis*) from the Walker Volcs, Australian Capital Territory, Australia; Silurian.



- **Arcticalymene** – ADRAIN and EDGECOMBE, 1997 (*viciousi*) from the Cape Phillips Formationm, Nunavut, Canada; Silurian.



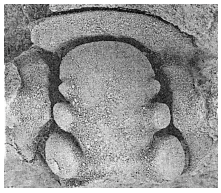
- **Calymene** – BRONGNIART, 1822 (*Calymene blumenbachii* BRONGNIART IN DESMAREST, 1817) from the Much Wenlock Limestone, England; Silurian.

- **Calymenella** – BERGERON, 1890 (*boisseri*) from the Glauzy Formation, Montagne Noire, France; Upper Ordovician – *Image unavailable*

- **Calymenesum** – KOBAYASHI, 1951b (*Calymene tingi* SUN, 1931) from the Shistzupu Formation, Guizhou, China; Middle Ordivician – *Image unavailable*

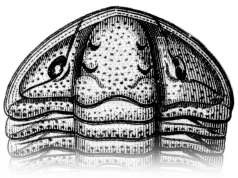
Table 2. Genera and name-bearing species of the type species of genera assigned to the family Calymenidae *(continued)*.

- **Colpocoryphe** – NOVAK in PERNER, 1918 (*Calymene (Synhomalonotus) arago* ROUAULT, 1849) from Ille-et-Villaeine, Brittany, France; Middle Ordovician – *Image unavailable*



- **Dekalymene** – CURTIS & LANE, 1998 (*Diacalymene crassa* SHIRLEY, 1936) from the Haverford Mudstone Formation, England; Silurian.

- **Diacalymene** – KEGEL, 1927 (*Calymene diademata* BARRANDE, 1846a) from the Lite Formation, Czech Republic; Silurian – *Diacalymene crassa shown*.



- **Flexicalymene** – SHIRLEY, 1936 (*Calymene blumenbachii var. caractaci* SALTER, 1865) from Marshbrookian, England; Upper Ordovician.

- **Gravicalymene** – SHIRLEY, 1936 (*convolva*) from the Crûg Limestone, Wales; Upper Ordovician.

- **Limbocalymene** – MAKSIMOVA, 1978a (*Calymene kokbaitalensis* MAKSIMOVA, 1968) from central Kazakhstan; Lower Devonian – *Image unavailable*

- **Linguocalymene** – TOMCZYKOWA, 1991 (*Spathacalymene linguata* TOMCZYKOWA, 1970) from the Cucullograptus hemiaversus Zone, Mielnik borehole, Poland; Silurian – *Image unavailable*

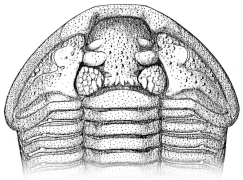
- **Liocalymene** – RAYMOND, 1916 (*Hemicrypturus clintonii* VANUXEM, 1842) from the Clinton Group, New York, USA; Silurian – *Image unavailable*

Table 2. Genera and name-bearing species of the type species of genera assigned to the family Calymenidae *(continued)*.

- **Metacalymene** – KEGEL, 1927 (*Calymene baylei* BARRANDE, 1846) from the Kopanina Formation, Czech Republic; Upper Silurian.

- **Neseuretinus** – DEAN, 1967 (*Neseuretus (Neseuretinus) turcicus*) from the Bedinan Formation, SE Turkey; Upper Ordovician.

- **Neseuretus** – HICKS, 1873 (*ramsayensis*) from the Ogof Hên Formation, Wales; Lower Ordovician.



- **Nipponocalymene** – KANEKO, 1985 (*hamadai*) from the Kitakami Mountains, NE Japan; Middle Devonian.

- **Onnicalymene** – DEAN, 1962a (*Flexicalymene onniensis* SHIRLEY, 1936) from the Onny Formation, England; Upper Ordovician.

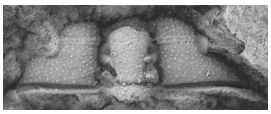
- **Papillicalymene** – SHIRLEY, 1936 (Calymene papillata LINDSTRÖM, 1885) from the Hemse Formation, Gotland, Sweden; Upper Silurian – *Image unavailable*

- **Paracalymene** – PILLET, 1968 (*Calymene bureaui* PENEAU, 1928) from Calcaires d'Erbray, Loire-Atlantique, France; Lower Devonian – *Image unavailable*

Table 2. Genera and name-bearing species of the type species of genera assigned to the family Calymenidae *(continued)*.

- **Platycalymene** SHIRLEY, 1936 (*Asaphus duplicatus* MURCHISON, 1839) from the Chirbury Formation, Shelve, England; Upper Ordovician.

- **Pradoella** – HAMMANN, 1977 (*pradoi*) from the Neseuretus Tristani Shales, Sierra Morena, Spain; Middle Ordovician – *Image unavailable*

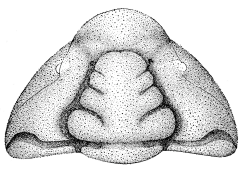


- **Protocalymene** – ROSS, 1967 (*mcallisteri*) from the Antelope Valley Formation, California, USA; Middle Ordovician – *Protocalymene sp. nov.* from Fortey and Droser (1997) used in place of the holotype *P. mcallister*

- **Reacalymene** – SHIRLEY, 1936 (*limba*) from the Glyn Gower Siltstone Formation, Wales; Upper Ordovocian – *Image unavailable*

- **Reedocalymene** – KOBAYASHI, 1951b (*Calymene unicornis* REED, 1917) from the Shidian Formation, Yunnan, China; Middle Ordovician – *Image unavailable*

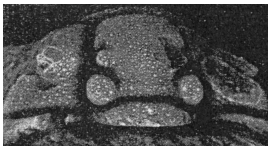
- **Salterocoryphe** – HAMMANN, 1977 (*Calymene salteri* ROUAULT, 1851) from the Schistes à Calymènes, Brittany, France; Middle Ordovician.



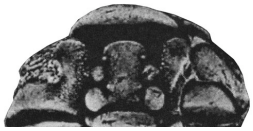
- **Sarrabesia** – HAMMANN & LEONE, 1997 (*teichmuelleri*) fom the Punta Serpeddi Formation, Sardinia, Italy; CALYMENIDAE; Upper Ordovician.

Table 2. Genera and name-bearing species of the type species of genera assigned to the family Calymenidae *(continued)*.

- **Spathacalymene** – TILLMAN, 1960 (*Calymene nasuta* ULRICH, 1879) from the Salamonie Dolomite, Indiana, USA; Silurian.



- **Sthenarocalymene** – SIVETER, 1977 (*lirella*) from the Vollen Formation, Norway; Upper Ordovician



- **Tapinocalymene** – SIVETER, 1980 (*Calymene nodulosa* SHIRLEY, 1936) from the Coalbrookdale Formation, England; Silurian

- **Thelecalymene** – WHITTINGTON, 1971b (*Calymene mammillata* HALL, 1861b) from the Maquoketa Formation, Iowa, USA; Upper Ordovician – *Image unavailable*

- **Vietnamia** – KOBAYASHI, 1960c (*Calymene douvillei* MANSUY, 1908) from the Nam Ho Shale, Vietnam; Middle Ordovician – *Image unavailable*

What becomes obvious is that many new genera have been described from very little material. Fortey and Droser (1997) described a new species of *Protocalymene*, stating, "Although undoubtedly an undescribed species, the sparse material obliges us to leave it under open nomenclature. As probably the oldest North American calymenid, it is of considerable interest. The type species of *Protocalymene* was described by Ross (1967) from silicified material, all of it rather small." Not only are holotypes, syntypes, and lectotypes of many of the type species incomplete specimens, they are also deformed.

In his study titled *Trilobite Taphonomy and Taxonomy: A Problem and Some Implications*, Nigel Hughes (1993) writes, "Numerous systematic papers discuss how preservation affects particular characters or character sets. Examples include the effects of compaction on sclerite morphology in specimens preserved in fine grain clastic sediments (e.g., Kiaer, 1917; Fortey, 1974), differences between carbonate and clastic preservation (e.g., Taylor, 1978), the differences in the morphology of internal and external molds (e.g., Jell, 1985), and how taphonomic artifacts have been mistaken for biological features."

In order to best overcome these obstacles, it is best to limit taxonomic diagnoses to only those characters that have a high preservation potential. However, this results in a restricted and inferior character set. Hughes (1993) goes on to suggest that, ". . . systematists could pay more attention to the completeness and taphonomic condition of their material before making taxonomic assessments." Failure to do so has lead to the over-inflation of genera within the Calymenidae family. Because the Calymenidids are high in diversity, but low in disparity, many species within a genus are as morphological diverse as the genera.

As shown in Figure 14 and 15, the morphological similarities between species of *Calymene*, *Flexicalymene*, and *Gravicalymene* are about as obvious as the differences in morphology within a single calymenid genus, *Flexicalymene*. This is not only evident in *Flexicalymene*, but is also in different species of *Gravicalymene*, *Onnicalymene*, and *Arcticalymene*. In contrast, the differences in the morphological characteristics of three of the species in *Arcticalymene* (see Figure 16) are greater than the differences separating the genera *Apocalymene, Calymene, Flexicalymene, Gravicalymene,* and *Sthenarocalymene*.

In one of the first attempts to reverse the over-inflation of the family Calymenidae, Holloway (1980) reassigned the newly described *Apolcalymene* (Chatterton & Campbell, 1980) as a synonymous of *Sthenarocalymene*. While outlining his reasons for rejection of *Apocalymene*, Holloway stated, " Chatterton AND Campbell (1980) included in their new genus *Apocalymene*

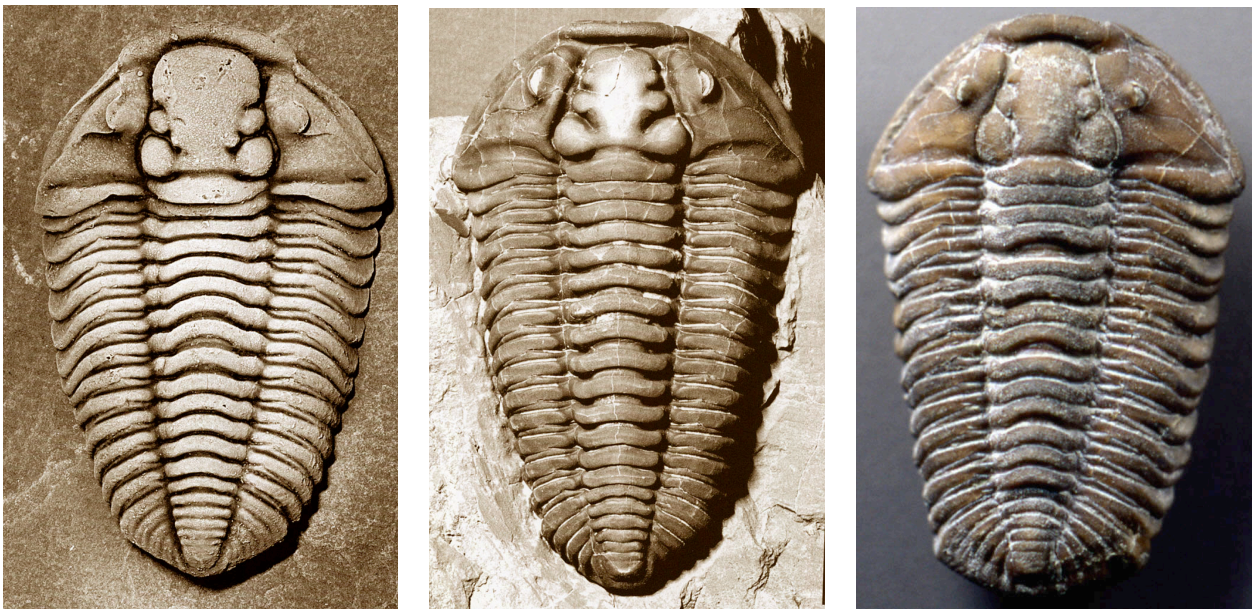


Figure 14. Morphological similarities among different species within the Calymenidae – *Calymene niagarensis* (l), *Flexicalymene meeki* (c), and *Gravicalymene abbreviata* (r).

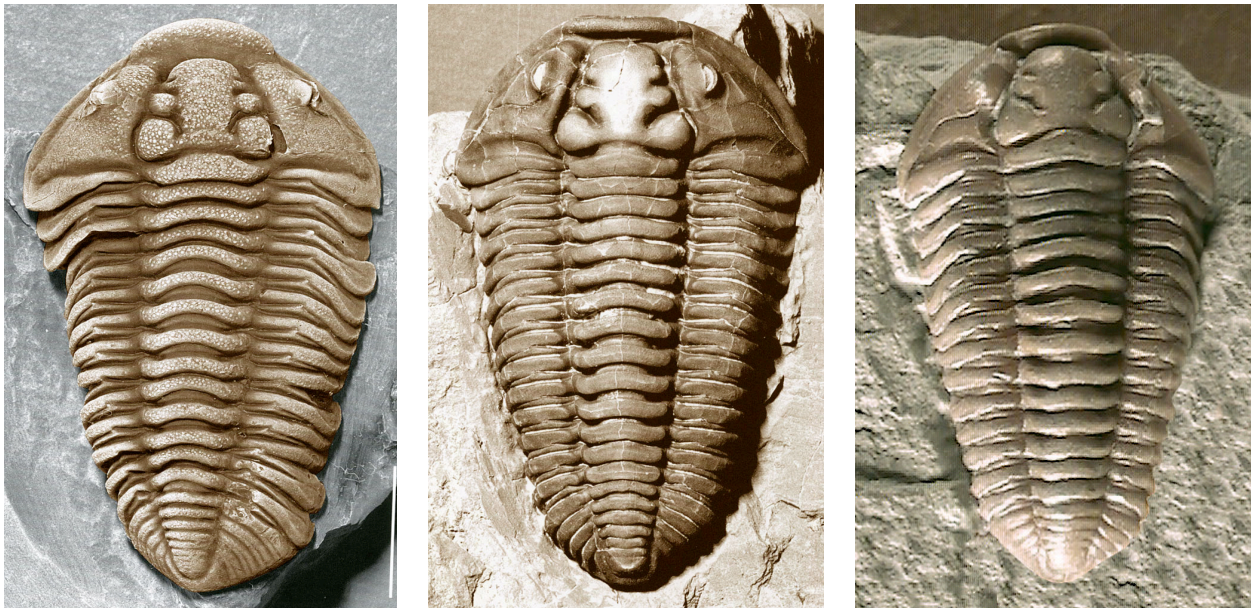


Figure 15. Morphological differences among different species within the same genus, *Flexicalymene* – *F. senaria* (l), *F. meeki* (c), and *Flexicalymene retrorsa* (r).

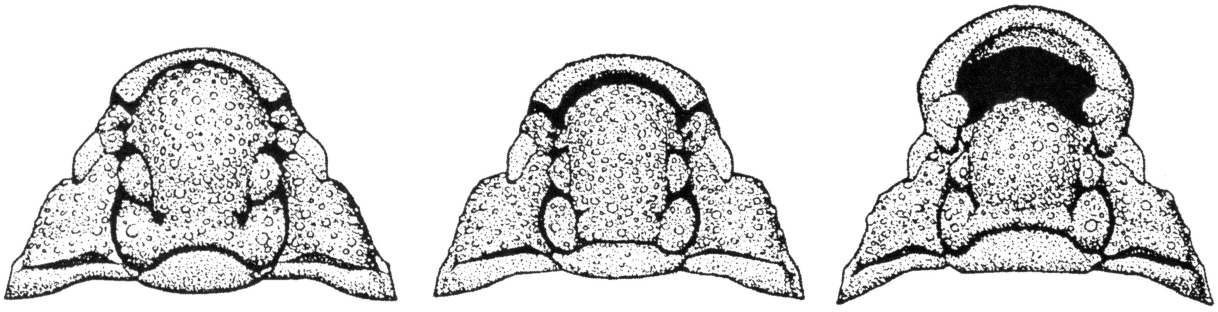


Figure 16. Differences between the shapes of the cephalon, glabellar shape, glabellar lobes, preglabellar field, and occipital ring within the genus *Arcticalymene* (Adrain and Edgecomb, 1997).

various Silurian and Early Devonian species that previously had been referred to either *Gravicalymene* or *Flexicalymene*. They listed in the diagnosis a relatively large number of features, many of which are present also in other calymenids. They stressed however, that it was the particular combination of characters they considered to be diagnostic. Whittington (1971) noted that in calymenids similar characters seem to have appeared at diffcrent times in apparently distinct stocks. Thus basing genera on character combinations, rather than on relatively few features that are considered to be individually diagnostic, may be advantageous. Unfortunately this has, to date, generally not proved possible and many calymenid genera are defined mainly on the presence or absence of genal buttresses, the shape of the glabella, and the profile of the anterior border.

Many post-Cambrian trilobite families have already undergone systematic revision, but the Calymenidae is still in need of revision. This study paves the way for a complete revision in a future study.

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METHOD OF STUDY

> "Trilobite classification systems have been claimed as 'natural" at least since the time of Salter (1864). Different authors have pursued their individual meanings of 'natural', although most have claimed that their classifications also reflect phylogeny. Two approaches to phylogenetics are representative: the tree-based, or stratigraphic approach, and the key-character approach respectively. The former is exemplified particularly by Cambrian specialists such as Franco Rasetti. The intention is to reproduce the actual tree of descent by means of stratigraphic and evolutionary series of species – the classification is imposed after the reconstruction of the tree. The key character approach identifies characters which are considered to be reliable indicators of descent – synapomorphies in modern understanding" (Fortey, 1997)

Previous studies – and subsequent new species decriptions – have been based wholly on visual differences in specimens. Trilobites have a complex morphology and a long geological history with an apparently good fossil record but their systematics are still in an unsatisfactory state (Fortey, 2001). The approach to classification and phylogenetics in trilobite studies has ssen a pardigm shift over the past 75 years.

Early classical evolutionary taxonomy was based on primitive morphological homologies (Fortey, 2001). The stratigraphic paradigm began in the 1930s with the extensive publication of descriptive papers of North American trilobites. Under this paradigm, stratigraphic collecting to reconstruct phylogenies became a "condition without which it could not be" classification. Implied in many of these descriptions, and expressed in some, is the "notion that phylogeny and taxonomy may best be determined by reference to stratigraphical succession" (Fortey, 2001). Many of the

calymenid trilobites were described during this time. Fortey (2001) went on to say that "trilobite classification based on the reconstruction of stratigraphy-based trees has not worked."

Through the development of cladistic methods – character-based parsimony – in the 1970s and 1980s came the "cladistic paradigm." An early study was that of Fortey and Chatterton (1988) who used computer-based parsimony analysis to reexamine relationships in Asaphida. Since then, extensive work has been performed on several groups, most notably Phacopina, Olenellida, Trinucleidae, and Encrinuridae. While the latter two did not result in much new insight on generic relationships within these respective families, the former two brought new awareness of evolutionary trends in trilobites.

A consistant problem with objective character-based analysis is the subjective nature of description. As with other automated methods, "garbage-in, garbage-out" applies to cladistics. When faced with the problem of describing the shape of the cephalon, what separates a semicircular shape from a rounded shape? What is the true difference between a "bell-shaped" glabella and a "tapered" glabella? Analysis (and therefore definition) of both depends on the analytical mindset of the scientist either describing the species, or reading about it. In this study, the subjectiveness has been removed from the character descriptions by using a combination of morphometric analysis tools and computer-based phylogenetics to reconstruct the evolutionary trends of the genera under analysis.

The question remains – regardless of what methods are used – what amount of characteristic differences warrant a new genus. Genera should not be defined by one character, but by a group of carefully chosen characters (Winston, 1999). The members of a genus do not have to share all characters however. One or more species in a genus may lack one or more of the diagnostic characters, or may have a character present, but in a modified form. In cases where modifications are slight, it is better to revise the genus than to create a completely new genus (Mayr and Ashlock, 1991). In the absence of genetic sequence data – such as the case in paleontology – morphometrics becomes key in species description and identification.

Genera Chosen for Study

Initially, the goals of the study were to evaluate the entire family Calymenidae. After careful consideration, it was determined that it would be more practical to complete the work with a sample group from the family. First and foremost, it was important to include those genera that the species *"Calymene" celebra* has been assigned to (informally as well as formally) over the past century. These include *Calymene, Flexicalymene, Gravicalymene,* and *Sthenarocaymene*. Second, genera that had been reassigned from the genus *Calymene* to a new genus were then included: *Alcymene, Diacalymene, Metacalymene,* and *Tapinocalymene*. Third, a species that had been reassigned twice – once from *Calymene* to *Flexicalymene*; and then again to a new genus – was included: *Onnicalymene*. A relatively new addition to the family, *Nipponcalymene* was added, as well as two genera that are distinctly different were included as control specimens: *Spathacalymene,* which has a spatulate anterior border, and *Arcticalymene* which has a tapered cephalon and oversized glabella.

Cladistics, a phylogenetic technique, requires the use of an outgroup to determine the polarity, or direction of change in character traits. An outgroup is a taxon related to the ingroup (the taxa under study), but showing all characteristics in their ancestral (primitive) or pleisiomorphic condition. In the real world, it is impossible to be certain whether the traits expressed in the outgroup are all truly primitive. In the case of the calymenids, a simple ptychopariid trilobite, (*Elrathia*), representative of the preserved root stock for the calymenids, was selected for the outgroup.

An evolutionary connection between the order Ptychopariida and the order Phacopida (including the calymenids) has long been assumed. One recent study suggests a direct link between the Ptychopariida and the Phacopida (see Figure 17), including *Calymene* and its close relatives.

Fortey (in Kaesler, 1997) stated in the revised trilobite volume of the *Treatise on Invertebrate Paleontology*, "It is possible Phacopida was derived from a libristomate ancestor . . . Ptychopariida includes only libristomates." The most primitive (pleisomorphic) families are lumped into the suborder Ptychopariina, which is dominated by families having the typical morphology as

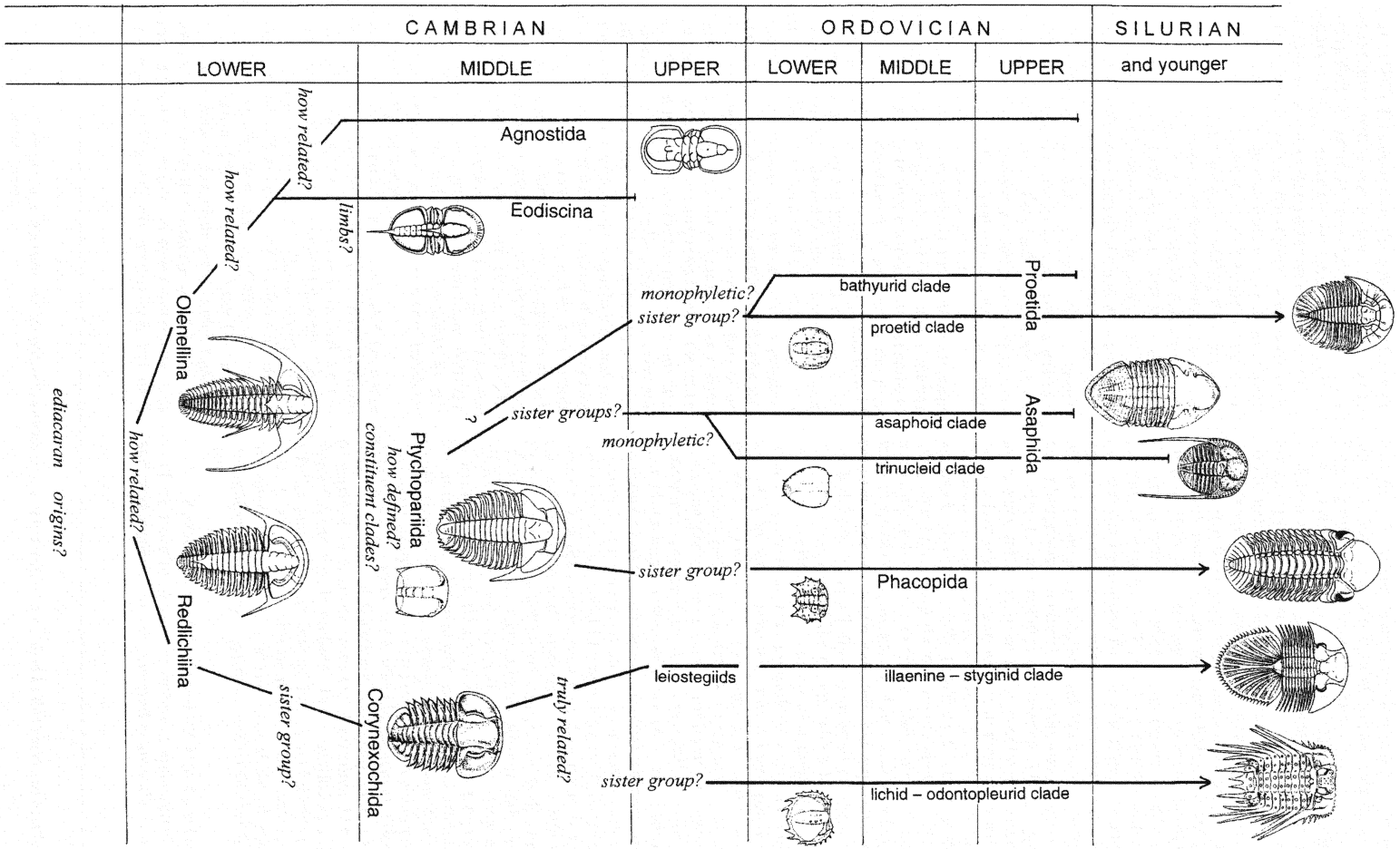


Figure 17. One scientific hypothesis on the trends of trilobite evolutionary relationships (Fortey, 2000).

exemplified by *Ptychoparia* itself or *Elrathia*." It is because of this possible link that *Elrathia kingi* (see Figure 18) was chosen as the outgroup for this study.

Morphometric Analysis Tools – The study of paleontology involves many different types of data and requires compatible methods of analysis. Recent advances in software development have provided accessible quantitative data analysis for paleontologists. A key software package used in this study is PAST (PAleontological STatistics) developed by Øyvind Hammer and David A. T. Harper. Using PAST, I have been able to simultaneously evaluate contrasting datasets obtained with morphometric data.

Because genetic sequence data are generally absent, the use of morphometrics – the measurement of the shape and size of organisms or their parts – is crucial to the study of ancient life. Morphometrics has become a rapidly evolving discipline thanks in part to Raup's (1966) early work on the elaboration of morphospace, and Bookstein's work in 1991.

Figure 18. *Elrathia kingi*, repesentative of the outgroup used for analysis of the Calymenidaes.

Because classification uses both quantitative and qualitative data, the goal was to remove the subjective nature of qualitative data. By using morphometrics to help find similarities within shapes, description of the cephalon can be defined in absolute values instead of solely on subjective descriptions. Morphometric data can be classified in several different ways. For this study, univariate, bivariate, and multivariate data were compiled and used.

Univariate measurements such as length and width were required to determine some of the phylogenetic characters used in the cladistic analysis. Bivariate interval/ratio measurements were also required when comparing cephalon length/width ratios to help determine shape characteristics and similarities in form.

Multivariate morphometric measurements involve multiple variate data sets that are difficult to objectively visualize. Using digitized outlines, the cephalon and glabella shape are compared to other shapes in the study group and placed with those specimens having an "identical shape" (within limits). The shape of the eye and its placement in comparison to the glabellar lobes and location on the cephalon, as well as the location of sutures, the shape of the anterior border, fixigenia, and other key cephalic components are defined through coordinates of landmark analysis and compared with other specimens.

In landmark analysis, which differs from outline analysis, a number of homologous points – or landmarks – are defined. Each is a point an object that can be correlated across all specimens in the study. Although landmarks can be classified as anatomical, mathematical, or pseudo-landmarks, only anatomical points, well-defined points that are homologous from one specimen to the next, were used. The x,y coordinates of these points are digitized. These points are then compared statistically. One major advantage of landmark analysis is that its results are easier to interpret in geometric terms (Hammer and Harper, 2006).

When digitizing landmarks from a number of specimens, it is difficult, if not impossible, to ensure that each specimen is measured in the same position and orientation. In order to accurately

compare shapes, it is then necessary to translate the points by scaling and rotating specimens to a common size and orientation. To accomplish this, Procrustes fitting is used.

Once the data have been translated into a series of Procruteses-fitted landmarks, Principal Component Analysis (PCA) is used. PCA subtracts the mean shape, creating a data set of Procrustes residuals. Analysis on the variance-covariance matrix of these residuals then establishes shape variation. Since the principal components now correspond to displacement vectors for all landmarks away from the mean shape, they can be more easily visualized (Hammer and Harper, 2006).

Phylogenetic Analysis Tools – A phylogenetic disgram, such as a cladogram, is a visual represnetation of a hypothesis of evolutionary relationships. The purpose of phylogenetic (cladistic) classification is to recognize phylogenetic lineages, all of whose members are descended from a common ancestor. The common ancestor and all descendents form a monophyletic group or clade. Phylogenetic classification is concerned with grouping species into groups, all members of which share a common ancestry (Wiley, 1981). evolutionary categories. To accomplish this, cladistics relies on shared derived characters, or synapomorphies, to ascertain a shared ancestry between species.

The key to good phylogenetic analysis is the assembly of a set of characters that properly illustrate evolutionary trends within the ingroup. A given characteristic is only as good as its variables. It is important to remove any subjectiveness from said variables. The character matrix for this study is shown in Table 3.

Table 3. Morphological characters used in phylogenetic analysis.

For each character state, 0 represents the primitive (ancestral, or pleisiomorphic) state.

1 **Cephalic Shape (per PAST analysis)** – Cephalon outlines were digitized and grouped in PAST software according to general shape (see Figures 19 & 20).

0 Semicircle (*Elrathia*)
1 Spatulate (*Spathacalymene*)
2 Flattened Round (*Onnicalymene*)
3 Squared Taper (*Gravicalymene, Diacalymene, Arcticalymene, & Tapinocalymene*)
4 Tapered Round (*Alcymene & Nipponcalymene*)
5 Rounded (*Calymene, "Calymene" Celebra, Metacalymene, Flexicalymene & Sthenarocalymene*)

2 **Cephalic Ratio – Width to Length**
(Length = 1, therefore 1.33:1 would be coded as variable 1)

0 1.68 – 2.33
1 1.00 – 1.67
2 2.34 – 3.00
3 3.67 – 4.33
4 3.00 – 3.67
5 4.34 – 5.00

3 **Glabellar Shape (per PAST analysis)** – Glabella outlines were digitized and grouped in PAST software according to statistical/analytical shape (see Figures 21 & 22).

0 *Elrathia*
1 *Alcymene, Metacalymene, Onnicalymene, Tapinocalymene*
2 *Arcticalymene, Diacalymene*
3 *Calymene, "Calymene" celebra*
4 *Flexicalymene, Gravicalymene, Spathacalymene*
5 *Nipponcalymene, Sthenarocalymene*

4 **Glabellar Ratio – Width to Length**
(Length = 1, i.e. 1.33:1 would be coded as variable 4)

0 1.11 – 1.20
1 1.00 – 1.10
2 1.21 – 1.30
4 1.31 – 1.40
3 1.41 – 1.50
5 1.51 – 1.60

Table 3. Morphological characters used in phylogenetic analysis *(cont'd)*.

For each character state, 0 represents the primitive (ancestral, or pleisiomorphic) state.

5 Pygidial Ratio – Width to Length
(Length = 1, i.e. 1.33:1 would be coded as variable 7)
0 2.34 – 2.67
1 2.01 – 2.33
2 2.68 – 3.00
3 1.68 – 2.00
4 3.01 – 3.33
5 3.34 – 3.66
6 1.34 – 1.67
7 1.00 – 1.33
8 3.67 – 4.00

6 Pygidial Length Ratio – Axial lobe length to overall length (axial lobe length described as a percentage of the overall length. The greater the perecentage, the greater difference in length. A value of 1.00 – or 100% – would indicate that the terminal axial piece extends to the posterior margin).
0 1.41 – 1.50
1 1.21 – 1.30
2 1.00 – 1.10
3 1.11 – 1.20
4 1.31 – 1.40

7 Pygidial Width Ratio – Axial lobe width to overall width
(Width = 1, i.e. 2.33:1 would be coded as variable 8)
0 4.26 – 4.50
1 2.00 – 2.25
2 3.76 – 4.00
3 2.51 – 2.75
4 3.26 – 3.50
5 3.01 – 3.25
6 2.76 – 3.00
7 3.51 – 3.75
8 2.26 – 2.50
9 4.01 – 4.25

Table 3. Morphological characters used in phylogenetic analysis *(cont'd)*.

For each character state, 0 represents the primitive (ancestral, or pleisiomorphic) state.

8 Number of Axial Rings in Pygidium

0 4
1 10
2 6
3 8
4 7
5 5
6 9

9 Occipital Ring Shape (per PAST analysis) – Occipital ring outlines were digitized and grouped in PAST software according to general shape (see Figures 21 & 23).

0 *Elrathia, Arcticalymene, Onnicalymene*
1 *Calymene, Metacalymene, "Calymene" celebra*
2 *Alcymene, Diacalymene, Flexicalymene, Nipponcalymene, Spathacalymene, Sthenarocalymene, Tapinocalymene*

10 Anterior Lobe Description – As seen in the sagiital view (see Figure 25).

0 Shallow, drops sharply, overhangs preglabellar field (Frontal lobe length > 40% of glabellar length, slope greater than 60°)
1 Deep, drops sharply, overhangs preglabellar field (Frontal lobe length < 40% of glabellar length, slope greater than 60°)
2 Shallow, drops sharply, recurves into preglabellar field|
3 Deep, drops sharply, recurves into preglabellar field
4 Shallow, drops gradually, recurves into preglabellar field (Frontal lobe length < 40% of glabellar length, slope less than 60°)

11 Inclined Anterior Lobe – Is the anterior lobe inclined before it begins to drop towards the preglabellar field.

0 No
1 Yes

12 Preglabellar Field Edge Characteristic

0 Lip
1 Ridged
2 Rolled

Table 3. Morphological characters used in phylogenetic analysis *(cont'd)*.

For each character state, 0 represents the primitive (ancestral, or pleisiomorphic) state.

13 Preglabller Field Trend
- 0 Narrow and horizontal
- 1 Wide and horizontal
- 2 Curves dramatically upward, very wide in relation to glabella
- 3 Curves dramatically upward, wide in relation to glabella
- 4 Curves dramatically upward, narrow in relation to glabella
- 5 Curves gradually upward, very wide in relation to glabella
- 6 Curves gradually upward, wide in relation to glabella
- 7 Curves gradually upward, narrow in relation to glabella

14 Anterior Border Shape (per PAST analysis) – Anterior Border outlines were digitized and clustered in PAST software according to statistical/analytical shape (see Figures 21 & 24).
- 0 *Elrathia, Calymene, Flexicalymene, Tapincalymene*
- 1 *Metacalymene, Onnicalymene, Sthenarocalymene, "Calymene" celebra*
- 2 *Alcymene, Arcticalymene, Nipponcalymene*
- 3 *Diacalymene, Gravicalymene*
- 4 *Spathacalymene*

15 Eyes Opposite Glabellar Lobe #
- 0 Between L1 and L2
- 1 Between L2 and L3
- 2 L1
- 3 Between L3 and L4
- 4 L2
- 5 L4
- 6 L3

16 Pairs of Glabellar Lobes
- 0 2
- 1 3
- 2 4

17 Ratio Glabellar Lobes – L1 to L2 (L2 = 1, i.e. 1.33:1 would be shown as character 0)
- 0 1.00 – 1.67
- 1 4.34 – 5.00
- 2 2.34 – 3.00
- 3 3.00 – 3.67
- 4 3.67 – 4.33
- 5 1.68 – 2.33

Table 3. Morphological characters used in phylogenetic analysis *(cont'd)*.

For each character state, 0 represents the primitive (ancestral, or pleisiomorphic) state.

18 **Ratio Glabellar Lobes** – L2 to L3 (L3 = 1, i.e. 1.33:1 would be shown as 6)
- 0 Not Applicable
- 1 1.68 – 2.33
- 2 3.67 – 4.33
- 3 3.00 – 3.67
- 4 2.34 – 3.00
- 5 4.34 – 5.00
- 6 1.00 – 1.67

19 **Glabellar Lobe L1 Shape –**
(based on single-perspective ellipses angles 30° through 90°)
- 0 Rounded Quadrangle
- 1 81 – 90
- 2 41 – 50
- 3 61 – 70
- 4 51 – 60
- 5 71 – 80
- 6 31 – 40
- 7 Present but undefinable
- 8 Not present

20 **Intermediate Lobe** – Between L1 and L2
- 0 No
- 1 Yes

21 **Glabellar Lobe L2 Shape** –
(based on single-perspective ellipses angles 30° through 90°)
- 0 Not present
- 1 81 – 90
- 2 41 – 50
- 3 61 – 70
- 4 51 – 60
- 5 71 – 80
- 6 31 – 40
- 7 Present but undefinable
- 8 Rounded Quadrangle

22 **Intermediate Lobe** – Between L2 and L3
- 0 Not present
- 1 No
- 2 Yes

Table 3. Morphological characters used in phylogenetic analysis *(cont'd)*.

For each character state, 0 represents the primitive (ancestral, or pleisiomorphic) state.

23 Glabellar Lobe L3 Shape –
(based on single-perspective ellipses angles 30° through 90°)
0 Not present
1 81 – 90
2 41 – 50
3 61 – 70
4 51 – 60
5 71 – 80
6 31 – 40
7 Present but undefinable
8 Rounded Quadrangle

24 Glabellar Furrow F1 Shape
0 Shallow, transverse
1 Shallow, slightly bifurcate
2 Shallow, bifurcate
3 Shallow
4 Deep, transverse
5 Deep, slightly bifurcate
6 Deep, bifurcate
7 Deep
8 Distinct
9 Not present

25 Glabellar Furrow F2 Shape
0 Shallow, transverse
1 Shallow, slightly bifurcate
2 Shallow, bifurcate
3 Shallow
4 Deep, transverse
5 Deep, slightly bifurcate
6 Deep, bifurcate
7 Deep
8 Distinct
9 Not Applicable

Table 3. Morphological characters used in phylogenetic analysis *(cont'd)*.

For each character state, 0 represents the primitive (ancestral, or pleisiomorphic) state.

26 Glabellar Furrow F3 Shape

9 Shallow, transverse
1 Shallow, slightly bifurcate
2 Shallow, bifurcate
3 Shallow
4 Deep, transverse
5 Deep, slightly bifurcate
6 Deep, bifurcate
7 Deep
8 Distinct
0 Not present

27 Glabellar Lobe L1 Papillate

0 No
1 Yes

28 Glabellar Lobe L2 Papillate

0 No
1 Yes

29 Glabellar Lobe L3 Papillate

0 No
1 Yes

30 Buttress Attached to Fixed Cheek

0 No
1 Yes

31 Presence of Genial Spine

0 No
1 Yes

32 Facial Suture Type

1 Gonatoparian
2 Proparian
0 Opisthoparian

Shape Analysis – As previously stated, many of the characters used in this study are quantitative. But those defining shape similarities were qualitative, and required a way of transforming shapes into a quantitative state. This was accomplished by taking those shape criteria outlines and grouping them according to mathematical similarities using the PAST software. The characters requiring such conversion were:

1 Cephalic Shape (per PAST analysis)

3 Glabellar Shape (per PAST analysis)

9 Occipital Ring Shape (per PAST analysis)

14 Anterior Border Shape (per PAST analysis)

Photos of the name-bearing specimens were scanned into thecomputer from published papers and outlines were then created. These were then digitized as a series of pairs of x,y coordinates, entered into the PAST software, and grouped using r-mode cluster analysis. R-mode cluster analysis is a technique for identifying groups and subgroups in a multivariate dataset, based on a given distance or similarity measure, putting weight on groupings of taxa (Hammer and Harper, 2006). It is a method of data exploration and visualization. Instead of stating that a cephalon is semicircular or tapered (both of which are subjective), they are grouped based on their similarities in shape, regardless of that shape. While there may be a choice of methods for distance measurement, I used Euclidean distance – a simple measure of the linear distance between the two points x and y in multidimentional space:

$$ED = \sqrt{\sum (x_i - y_i)^2}$$

Cephalic Shape – Elliptical fourier analysis was first used to analyze cephalic shape. It was determined that this method of analysis was also interpreting the base (occipital border) of the cephalon in its calculations. Since this information would be determined in the analysis of the occipital ring shape, EFA was discarded. Cephalic shape indicates only the curvature of the cephalon

that is composed of the lateral border and anterior border and visual outline analysis was used in its place. Digitized outlines were plotted on a 2D graph and similar shapes grouped. Once a common grouping was achieved, then those members of that group were given a matching numerical variable and a descriptive shape. In the case of the cephalic outline, the following groups were found to exist:

Cephalic Shape (per PAST analysis) – Cephalon outlines were digitized and grouped in PAST software according to general shape (see Figures 18 & 19).

0 Semi-Circle (*Elrathia*)
1 Spatulate (*Spathacalymene*)
2 Flattened Round (*Onnicalymene*)
3 Squared Taper (*Gravicalymene, Diacalymene, Arcticalymene, & Tapinocalymene*)
4 Tapered Round (*Alcymene & Nipponcalymene*)
5 Rounded (*Calymene, "Calymene" celebra, Metacalymene, Flexicalymene & Sthenarocalymene*)

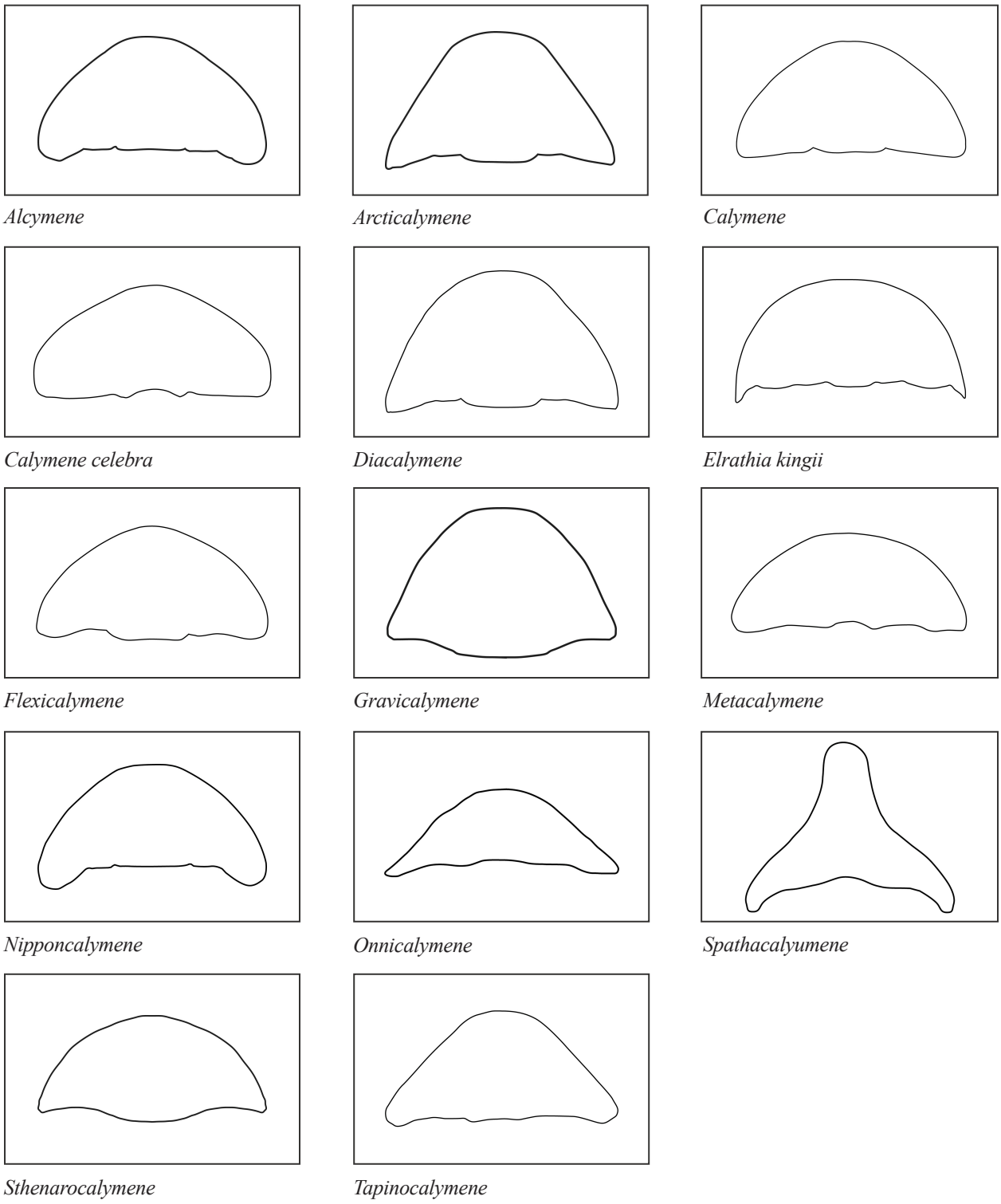


Figure 19. Cephalic outlines as drawn mostly from photographs of name-bearing types.

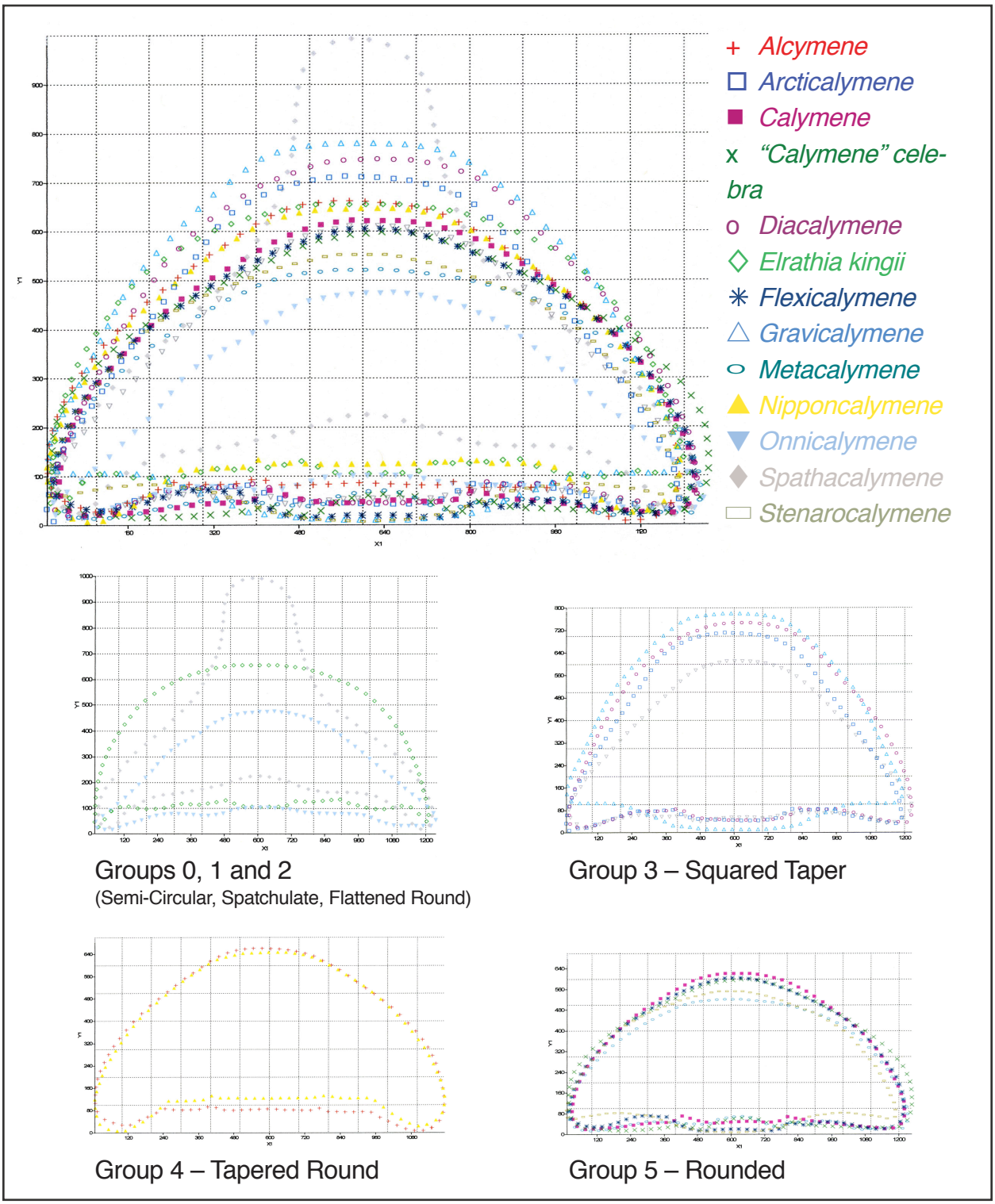


Figure 20. Grouping of cephalic outlines per PAST software.

Cranidial Shape – The shape of the anterior border, glabella, and occipital ring were also determined to be derived characters in the phylogentic study. Because these shape analysis groups were independent of any other characteristics, cluster analysis was used to determine groupings. Outlines were created from the name-bearing types where possible. If name-bearing types were not available, outlines were created from other specimens. The glabellar outline was drawn without the glabellar lobes. The lobe shapes were defined as an equivilant to an ellipsoidal shape based on an ellipsis drawn at angles bewteen 30° and 90° (a circle). Specific species within several genera were included for additional analysis.

Althought the outlines were drawn as one piece, representing cranidia (see Figure 20), they were broken down into individual components during analysis. The groupings were defined as follows:

Glabella Shaper (per PAST analysis) – Glabella outlines were digitized and grouped in PAST software according to analytical shape clusters (see Figures 20, 21).

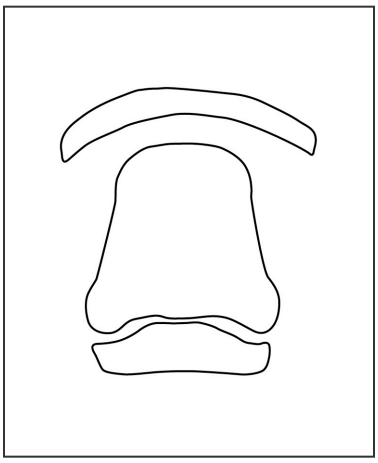
0 *Elrathia*
1 *Alcymene, Metacalymene, Onnicalymene, Tapinocalymene*
2 *Arcticalymene, Diacalymene*
3 *Calymene, "Calymene" celebra*
4 *Flexicalymene, Gravicalymene, Spathacalymene*
5 *Nipponcalymene, Sthenarocalymene*

Occipital Ring Shape (per PAST analysis) – Occipital Ring outlines were digitized and grouped in PAST software according to analytical shape clusters (see Figures 20, 22).

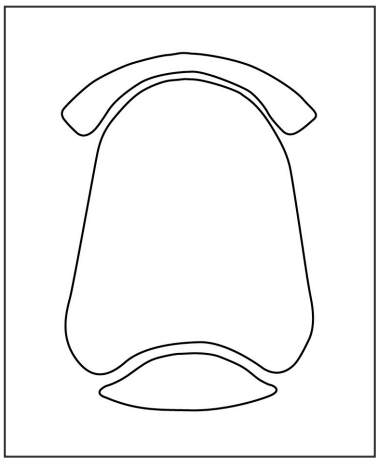
0 *Elrathia, Arcticalymene, Onnicalymene*
1 *Calymene, Metacalymene, "Calymene" celebra*
2 *Alcymene, Diacalymene, Flexicalymene, Nipponcalymene, Spathacalymene, Sthenarocalymene, Tapinocalymene*

Anterior Border Shape (per PAST analysis) – Anterior Border outlines were digitized and clustered in PAST software according to analytical shape clusters (see Figures 20, 23).

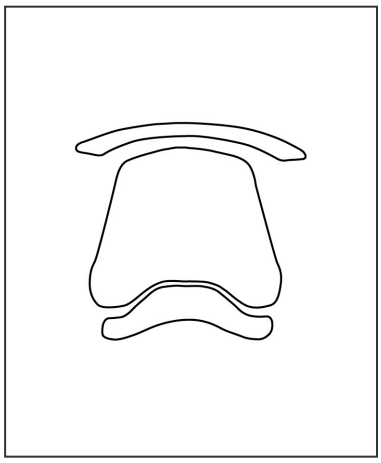
0 *Elrathia, Calymene, Flexicalymene, Tapincalymene*
1 *Metacalymene, Onnicalymene, Sthenarocalymene, "Calymene" celebra*
2 *Alcymene, Arcticalymene, Nipponcalymene*
3 *Diacalymene, Gravicalymene*
4 *Spathacalymene*



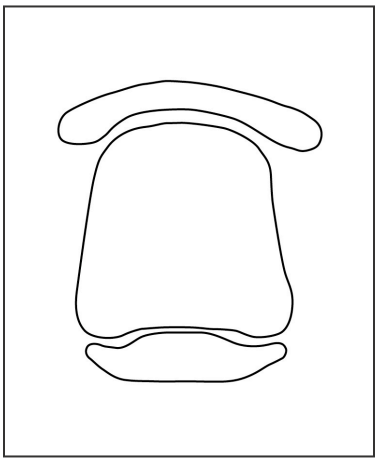
Alcymene



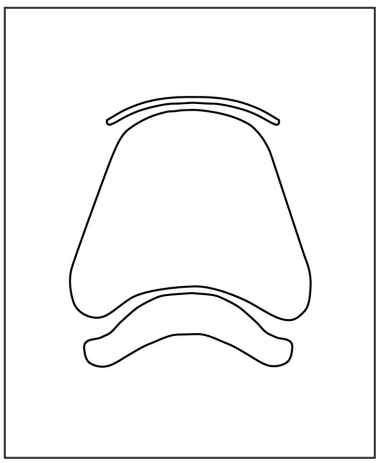
Arcticalymene



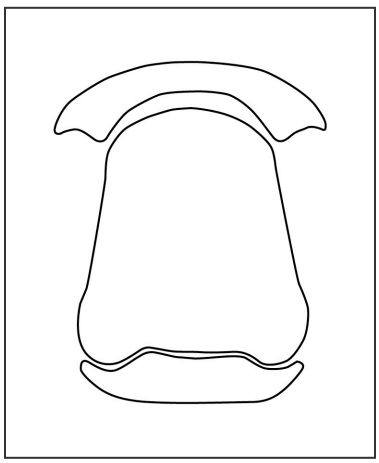
Calymene



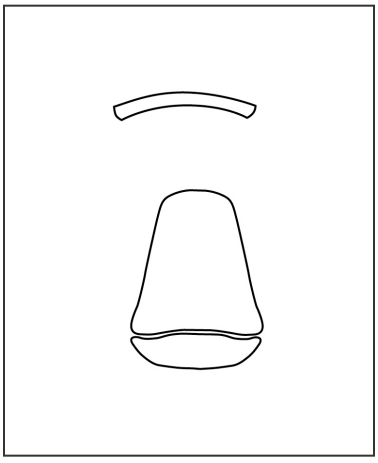
Calymene niagarensis



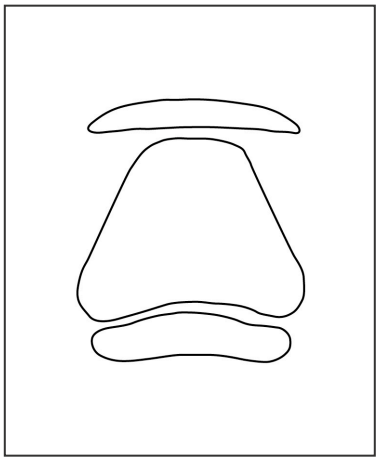
Calymene celebra



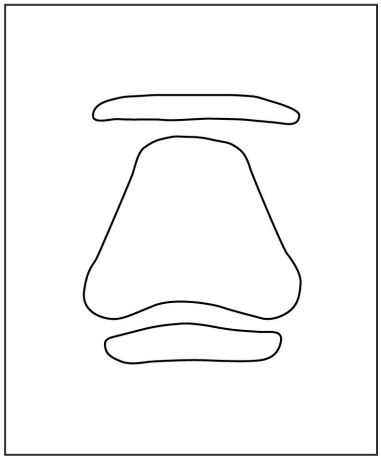
Diacalymene



Elrathia kingi

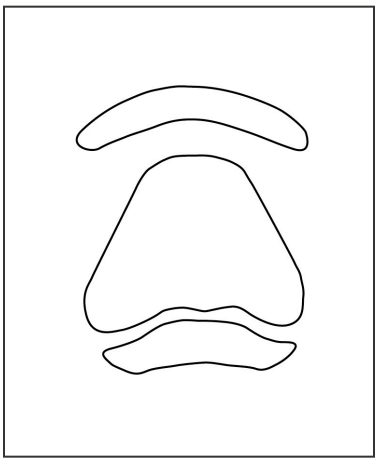


Flexicalymene

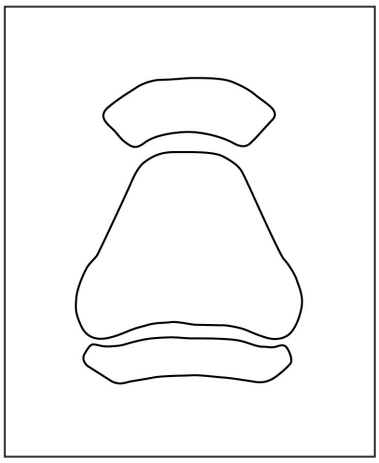


Flexicalymene meeki

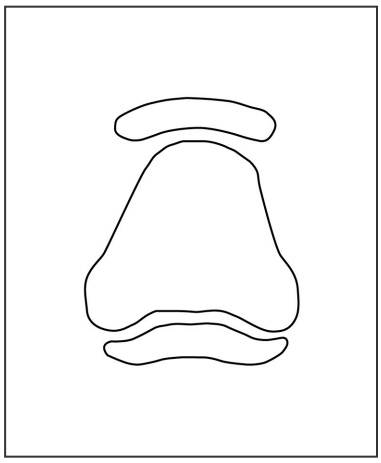
Figure 21. Anterior border, glabella, and occipital ring outlines (1 of 2)



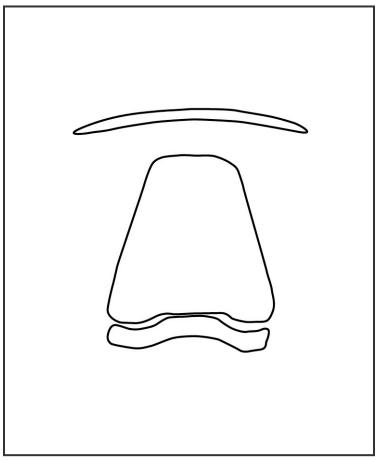
Flexicalymene senaria



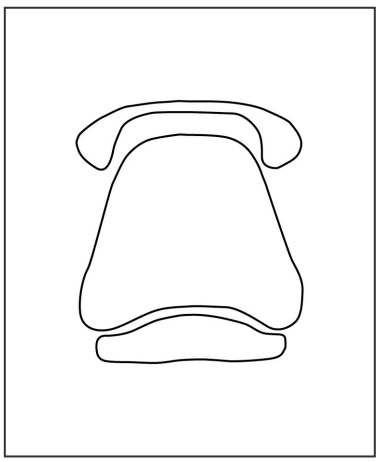
Gravicalymene



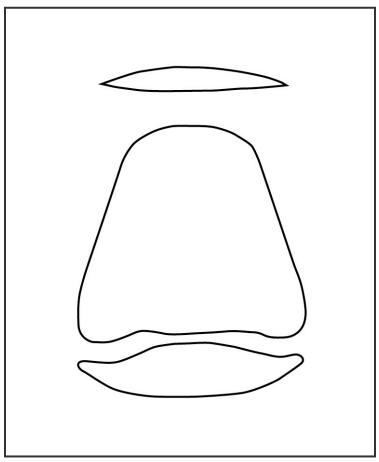
Gravicalymene abbreviata



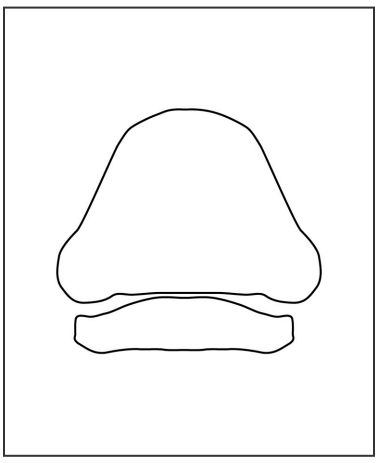
Metacalymene



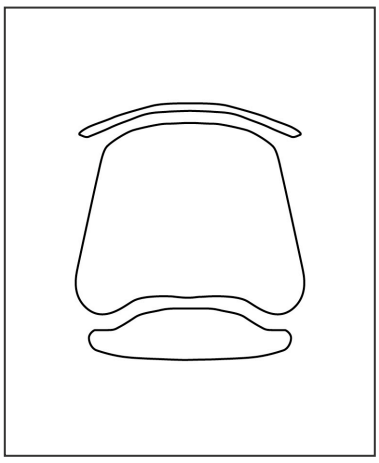
Nipponcalymene



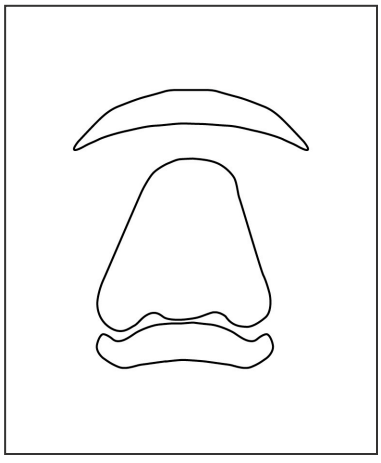
Onnicalymene



Spathacalymene

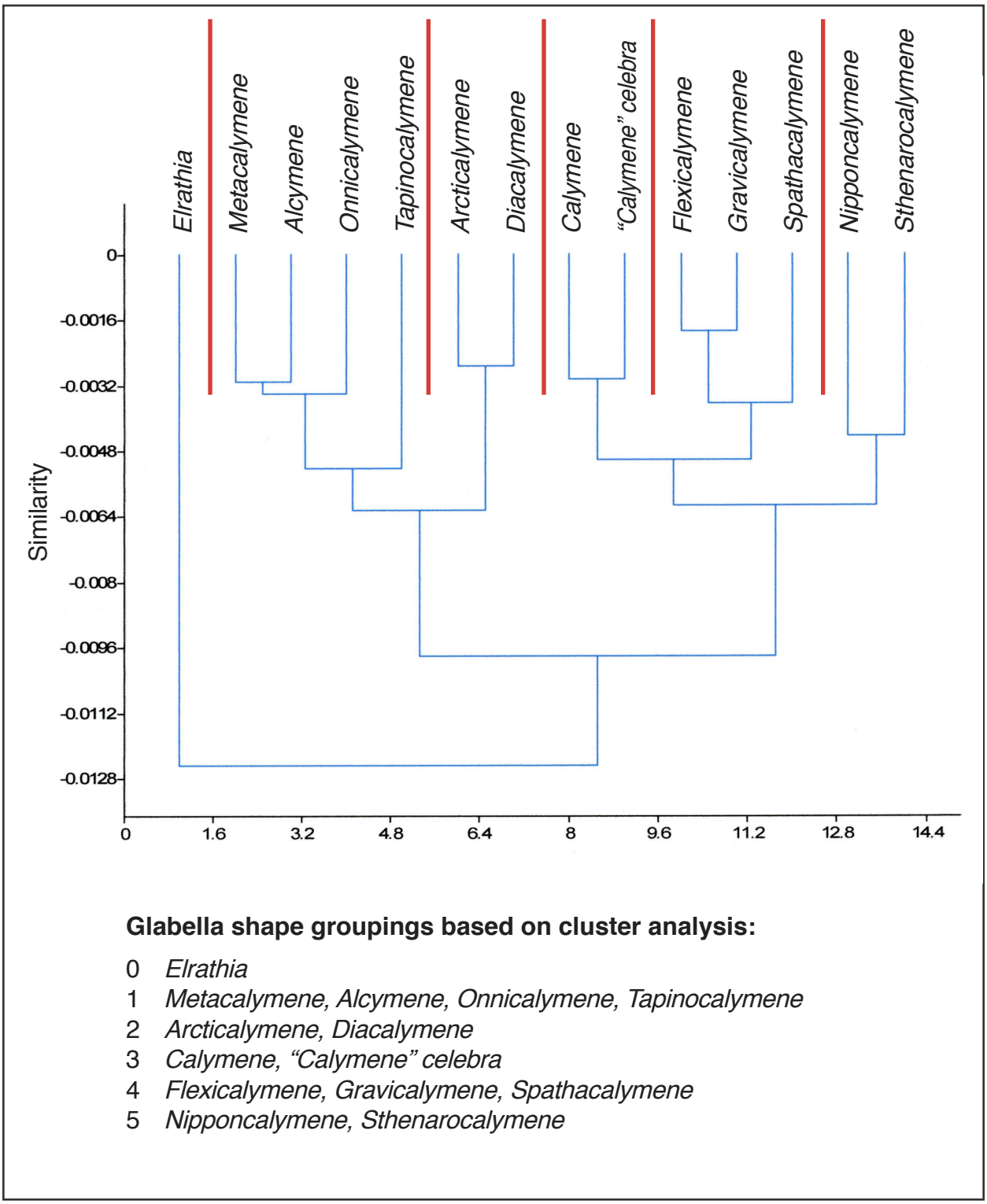


Sthenarocalymene



Tapinocalymene

Figure 21. Anterior border, glabella, and occipital ring outlines (2 of 2)



Glabella shape groupings based on cluster analysis:

0 *Elrathia*
1 *Metacalymene, Alcymene, Onnicalymene, Tapinocalymene*
2 *Arcticalymene, Diacalymene*
3 *Calymene, "Calymene" celebra*
4 *Flexicalymene, Gravicalymene, Spathacalymene*
5 *Nipponcalymene, Sthenarocalymene*

Figure 22. Denogram showing groupings of glabellar shape based on cluster analysis.

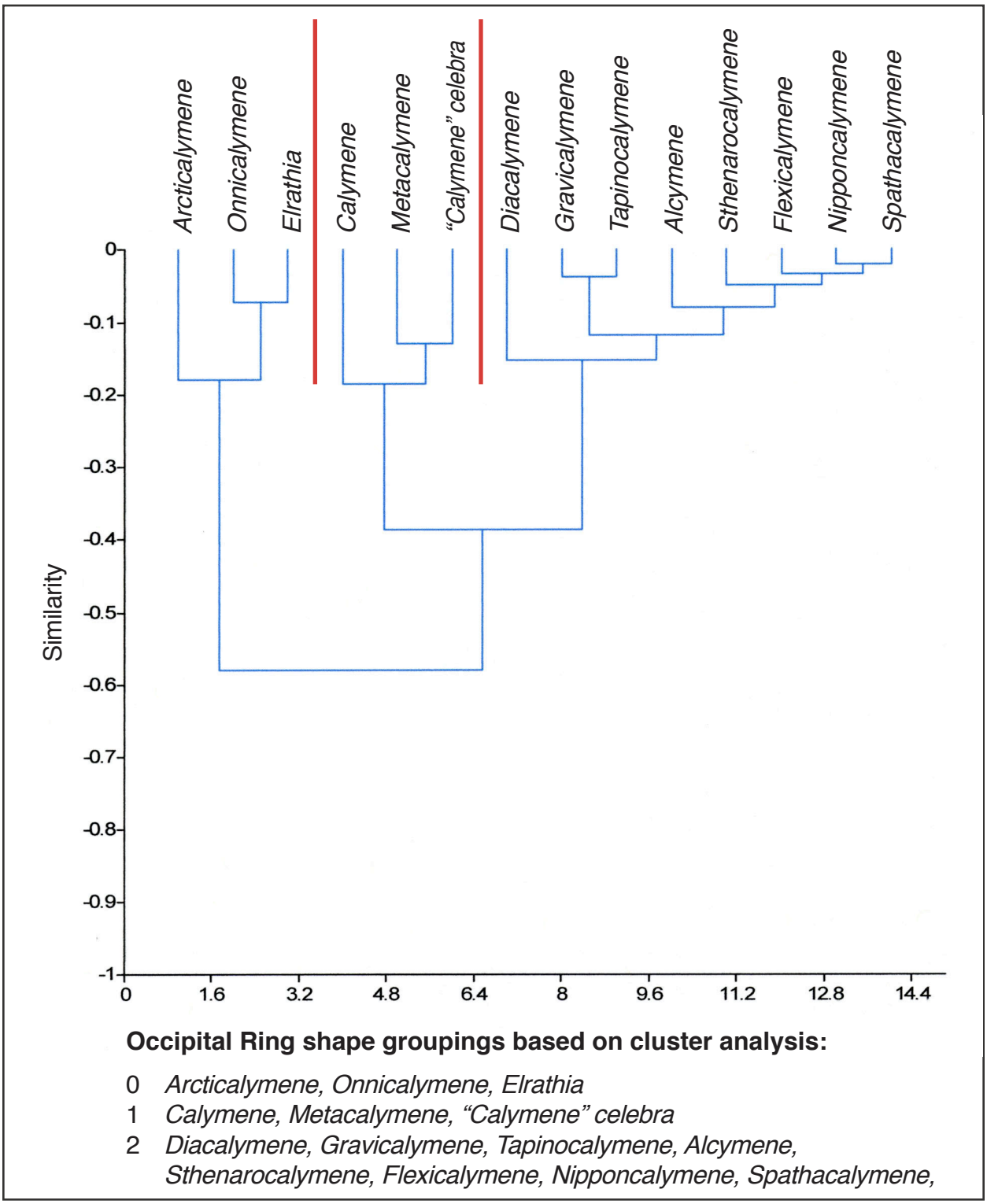


Figure 23. Denogram showing groupings of occipital ring shape based on cluster analysis.

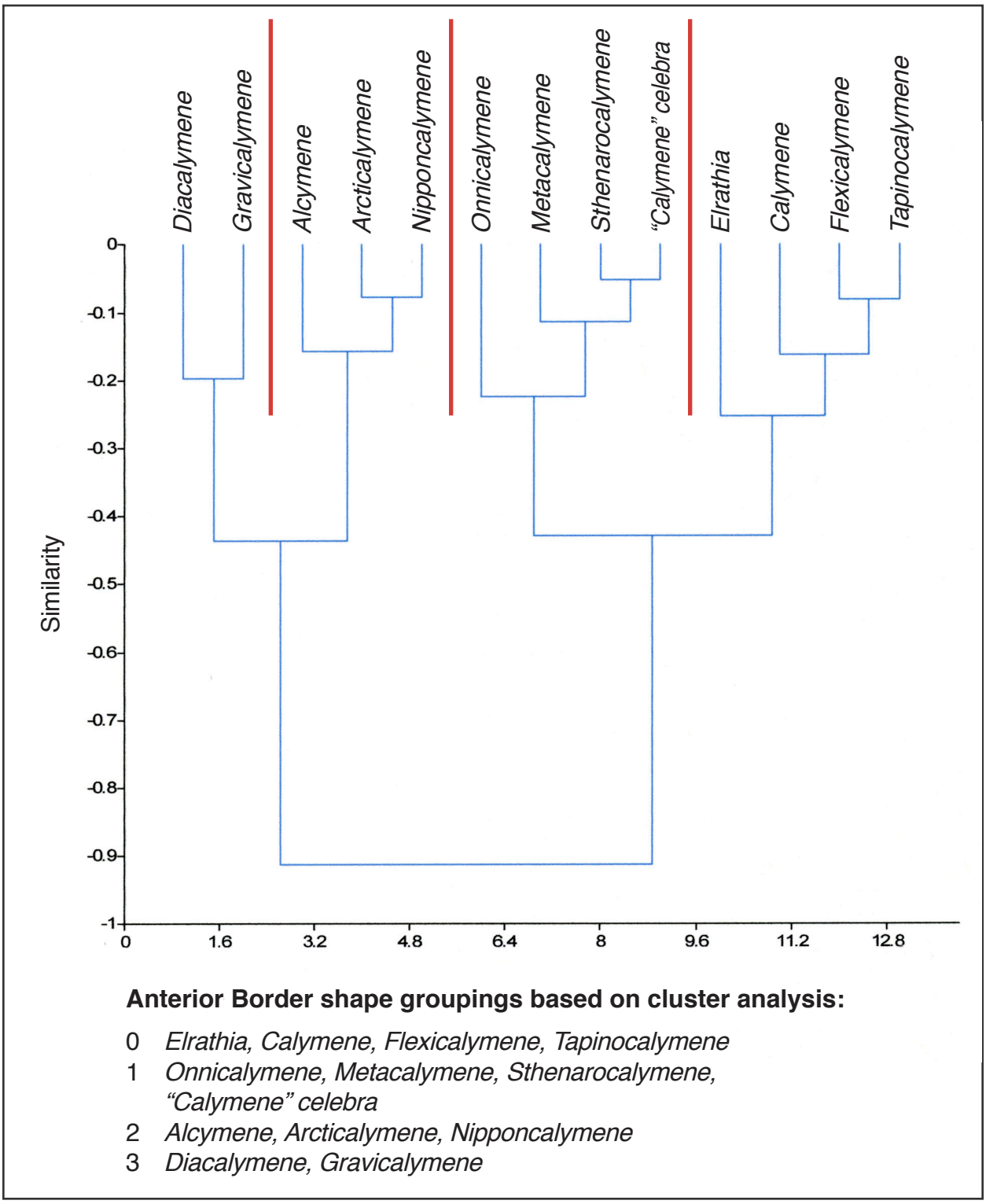


Figure 23. Denogram showing groupings of anterior border shape based on cluster analysis.

Anterior Lobe Description – In previous studies, the orientation of the anterior lobe was determined subjectively. From paper to paper there was no consensus for the format of description. Although I used terms such as "shallow", or "drops sharply," mathematical boundaries were set to eliminate the nomencalture used. All determinations are made from the sagiital view (see Figure 25).

The term "shallow" refers a frontal lobe length greater than 40% of the glabellar length. The term "deep" refers to a frontal lobe length less than 40% of the glabellar field. The terms "Drops Sharply" and "Drops Gradually" indicate a slope of greater than 60° and less than 60° respectively. The remainder of the descriptive language refers to whether the anterior lobe overhangs the preglabellar field (as shown in *Arcticalymene*, Figure 25) , or recurves into the preglabellar field (as shown in *Calymene*, Figure 25).

Anterior Lobe Description – As seen in the sagiital view (see Figure 25).

0 Shallow, drops sharply, overhangs preglabellar field
(Frontal lobe length > 40% of glabellar length, slope greater than 60°)

1 Deep, drops sharply, overhangs preglabellar field
(Frontal lobe length < 40% of glabellar length, slope greater than 60°)

2 Shallow, drops sharply, recurves into preglabellar field

3 Deep, drops sharply, recurves into preglabellar field

4 Shallow, drops gradually, recurves into preglabellar field
(Frontal lobe length < 40% of glabellar length, slope less than 60°)

Preglabellar Field Trend – Following Shirley (1936), trilobite workers have tended to adopt his proposal that the "trend" or shape of the preglabellar field was a derived character. The horizontal trend ranges from narrow (in relation to the frontal lobe) and horizontal (as seen in the sagiital view), as shown in *Elrathia* (see Figures 21 & 25), to wide and horizontal as shown in *Tapinocalymen*e. Those preglabellar fields that curve dramatically upward include the widths very wide (*Flexicalymene*), wide (*Gravicalymene*), and narrow (*Spathacalymene*). Those that have a more gradual rise include both a wide field (*Alcymene*) and a narrow field (*Calymene*).

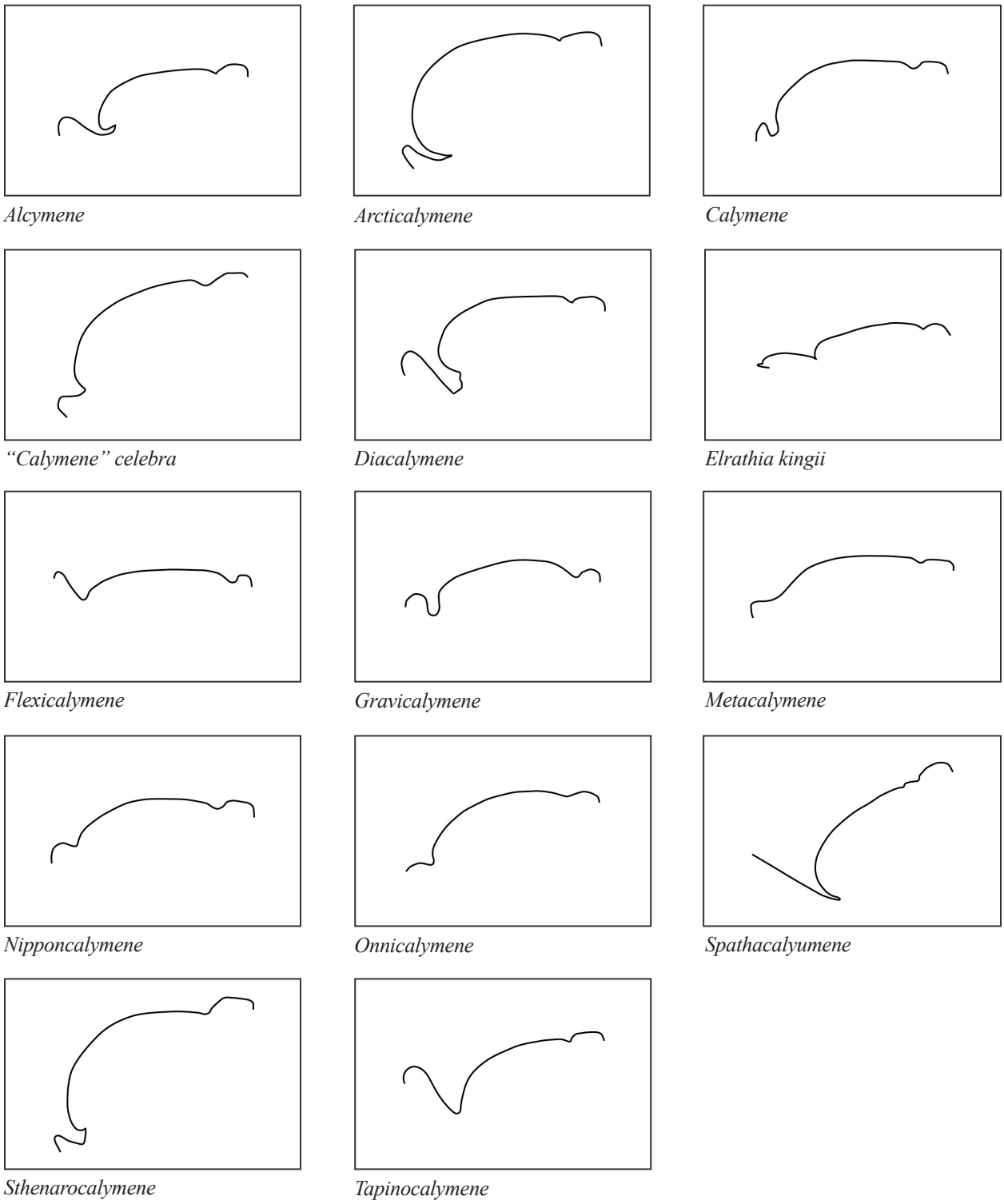


Figure 25. Profiles of cranidia including frontal lobe and preglabellar field (sagital view).

Preglabeller Field Trend

0 Narrow and horizontal
1 Wide and horizontal
2 Curves dramatically upward, very wide in relation to glabella
3 Curves dramatically upward, wide in relation to glabella
4 Curves dramatically upward, narrow in relation to glabella
5 Curves gradually upward, very wide in relation to glabella
6 Curves gradually upward, wide in relation to glabella
7 Curves gradually upward, narrow in relation to glabella

By assigning a character for both anterior lobe description, and preglabellar field trend, a complete objective description of the anterior border of each specimen can be accomplished. Another derived character was used in the past is a subjective description of the shape of the glabellar lobes. For the purposes of this study, the shape of the lobes was determined using a series of single-perspective ellipses. An ellipse is a conic section, the locus of points in a plane such that the sum of the distances to two fixed points is a constant. Ellipses can be drawn at different single-perspective angles. As the angle increases, the ellipse becomes more rounded. A 90° ellipse is in fact a circle (see Figure 26).

These ellipse angles were output on clear mylar at different sizes and overlaid on the photos of the specimens. Each of the glabellar lobes were then fit the closest ellipse angle. This value was recorded in the cladistic table.

Glabellar Lobe Shape (L1 hru L4 where applicable) –
(based on single-perspective ellipses angles 30° through 90°)

0 Rounded Quadrangle
1 81 – 90
2 41 – 50
3 61 – 70
4 51 – 60
5 71 – 80
6 31 – 40
7 Present but undefinable
8 Not present

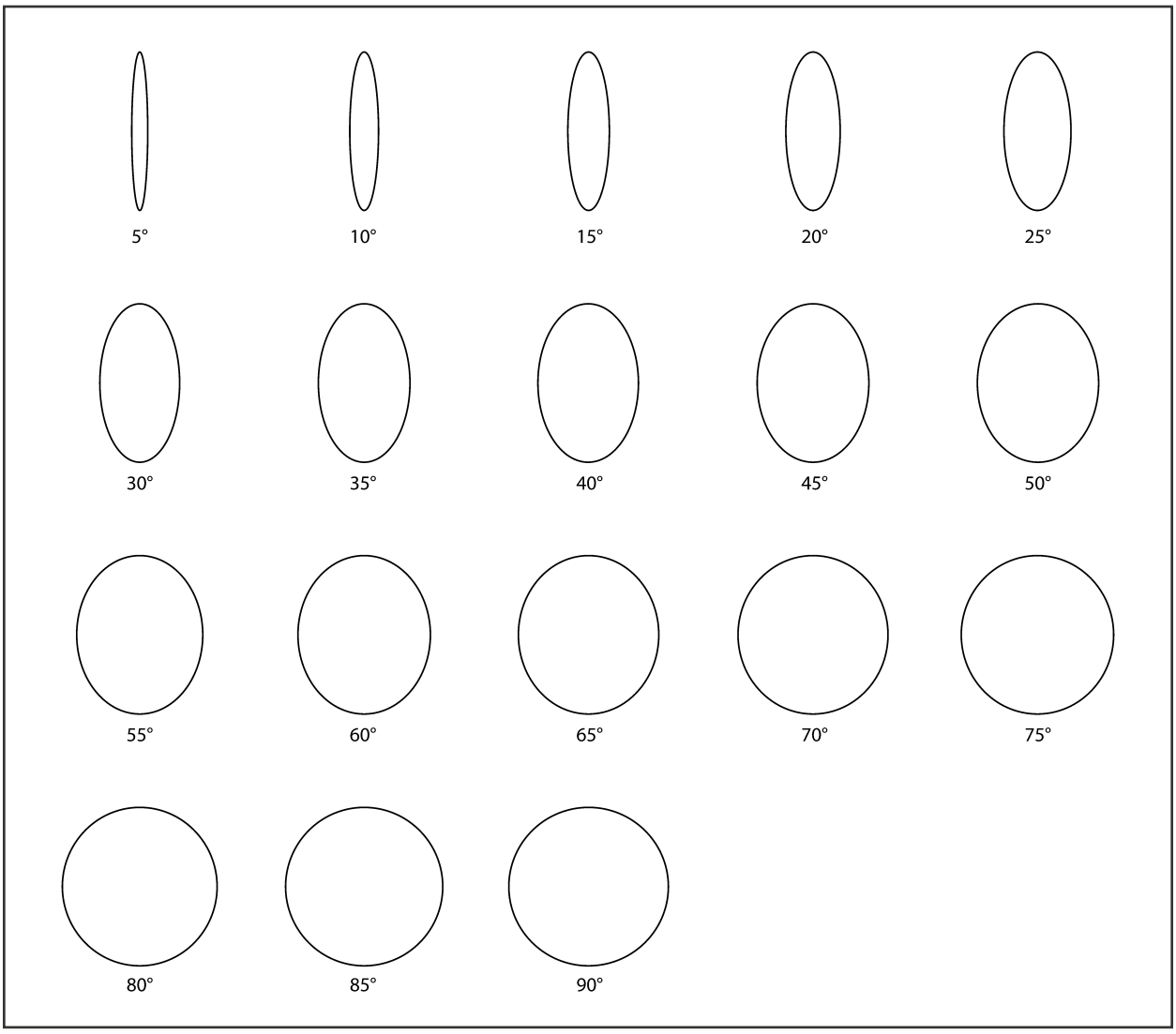


Figure 26. Single-perspective ellipse angles used to classify glabellar lobe shape.

Parsimony Analysis Procedure – The key to phylogenetic analysis is the creation of a character matrix with taxa in rows and characters in columns. Each cell in the matrix column contains numerical codes for the individual character states as described in Table 3. The number of characters and the distribution of character states between taxa will control the resolution of the parsimony analysis. It is necessary to specify a method for calculating the evolutionary "cost" of changes in a chararcter state from one taxon to another. They can be "ordered" where a change from state 0 to 2

"costs" more than a change from 0 to 1, but the same as a change from 2 to 0. Alternatively, they can be "unordered" meaning that all changes have an equal cost of one step. Unordered character states have the fewest assumptions and is the preferred of the two. This study used unordered character states.

Once the character matrix was complete (see Table 4), it was necessary to input this data into a specialized format. This was performed using MacClade (Maddison and Maddison, 2008) – a software tool for phylogenetic analysis. Although MacClade allows weighting of individual cahracters, in this study I chose to use all characters unweighted.

The data matrix was exported to *PAUP: Phylogenetic Analysis Using Parsimony* (Swafford, 2002) software. PAUP was designed for the inference of evolutionary trees and phylogenetic analysis using parsimony, maximum likelihood, and distance methods. Parsimony analysis involves finding evolutionary trees with a minimal length – the total number of character changes along the tree based on ordered or unordered character states. Because the shortest trees can be arbitrarily rooted (any taxon could be chosen as the most primitive by the software), it is necessary to root the tree by selecting an outgroup among the taxa. For this study, as previously stated, *Elrathia kingi* was choosen as the outgroup.

There is no simple method for finding the shortest trees directly. Calculations of a large possible number of trees (7.906×10^{12} – for N species, the number of possible trees = 1x3x5x7…x(2N-3) – have to be made to search for the shortest tree. This is accomplished using a variety of algorithms – exhaustive search, branch-and-bound, and heuristic algorithms.

An exhaustic search involves constructing all possible trees by sequential addition of taxa in all possible positions, and then calculating tree length. Although guaranteed to find the shortest trees, it is impractical because of the immense number of trees that are searched – over 700 trillion for 14 taxa.

By adding branch-and-bound algorithms to the exhaustive search, as taxa are added to a tree under construction, the tree length is continuously calculated even before it is complete. If the calculated tree length exceeds the shortest complete tree found so far, further calculations are

Table 4. Study genera character matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Elrathia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alcymene	4	0	1	1	7	2	8	2	2	1	0	2	6	2	4	1	0	4	3	1	3	2	7	5	4	8	0	1	0	1	1	1	0
Arcticalymene	3	1	2	2	7	2	1	4	0	1	1	0	6	2	4	2	0	1	2	1	4	1	7	5	4	8	0	1	1	1	1	1	0
Calymene	5	0	3	2	2	2	8	2	1	3	0	0	7	0	4	1	5	6	4	0	3	1	4	6	2	3	0	1	0	1	1	1	0
Diacalymene	3	0	2	1	7	2	1	4	2	1	0	1	2	3	4	1	0	4	4	1	2	1	2	5	6	3	0	1	0	1	1	1	0
Flexicalymene	5	0	4	1	2	2	6	2	2	4	0	0	3	0	4	1	0	6	4	0	2	1	2	6	7	7	0	0	0	0	1	1	0
Gravicalymene	3	1	4	2	6	2	3	2	2	2	1	2	4	3	4	1	3	6	2	1	2	2	7	6	5	8	0	0	0	0	1	1	0
Metacalymene	5	2	1	1	8	2	9	6	1	4	0	0	1	1	1	2	5	6	0	0	8	1	8	5	7	3	0	0	0	0	1	1	0
Nipponcalymene	4	0	5	1	1	2	6	1	2	4	1	2	1	2	4	1	5	1	2	1	6	1	6	6	7	3	0	1	0	1	1	1	0
Onnicalymene	2	4	1	3	3	2	6	5	0	3	1	2	1	1	4	1	5	6	0	1	2	1	6	6	6	7	0	0	0	0	1	1	0
Spathacalymene	1	1	4	3	3	3	8	5	2	1	0	3	5	4	4	1	0	3	3	1	4	1	7	6	7	3	0	1	0	1	1	1	1
Sthenarocalymene	5	0	5	3	6	1	8	5	2	1	0	0	7	1	4	1	5	6	3	0	3	1	7	5	4	3	0	0	0	0	1	1	0
Tapinocalymene	3	0	1	1	0	2	6	4	2	3	0	2	2	0	4	1	0	4	3	1	4	1	1	6	4	3	0	1	0	1	1	1	0
"Calymene" celebra	3	0	3	2	6	2	6	2	1	1	0	0	7	1	1	1	5	6	3	1	4	1	7	5	7	8	0	1	0	1	1	1	0

aborted. Branch-and-bound is also guaranteed to find all the shortest trees, and is the recommended algorithm for parsimony analysis. This study utilized the branch-and-bound method of tree construction.

Landmark Analysis – Landmark analysis was used to corraborate the findings of the cladistic analysis. In addition to the 14 specimens used in the cladistic analysis, four additional species-level specimens were chosen to determine similarities as well as dissimilarities within genera. These four species were *Flexicalymene meeki, Flexicalymene senaria, Calymene niagarenisis, and Gravicalymene abbreviata*.

Shirley (1936) spelled out the importance of the cranidium in trilobite studies. He had determined that the pygidia and thoraxes of calymenids were too similiar to be used in classification. Eighty-seven landmark points were chosen to best reflect the shape and landmark locations on trilobite cranidia (see Figure 27). These points were then digitized, translated to Procrustes fitted data, and then subjected to Principal Component Analysis. Scatter plots and cluster dendrograms were then created to find similarities and trends in the data.

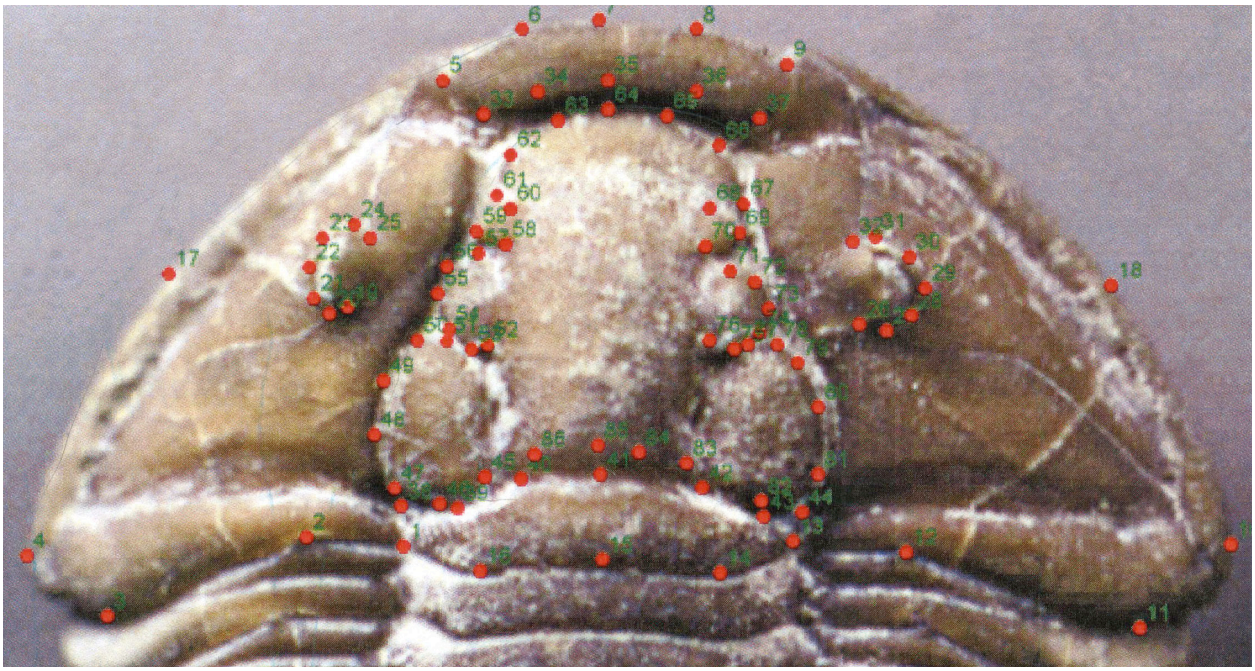


Figure 27. Location of landmark points on the cranidia.

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RESULTS

The quantitative analysis of calymenid trilobites was completed using both phylogenetic process utilizing cladistics, and morphometric analysis utilizing landmark data. Results from both tests were compared and collaborated where possible.

Phylogenetic Analysis – Cladistic analysis of the character matrix using PAUP yielded three trees calculated as having the shortest branches (see Figures 28 and 29). Tree 1 and Tree 2 are identical except for the branching of *Nipponcalymene*. In Tree 1 (Figure 28), has *Nipponcalymene* and

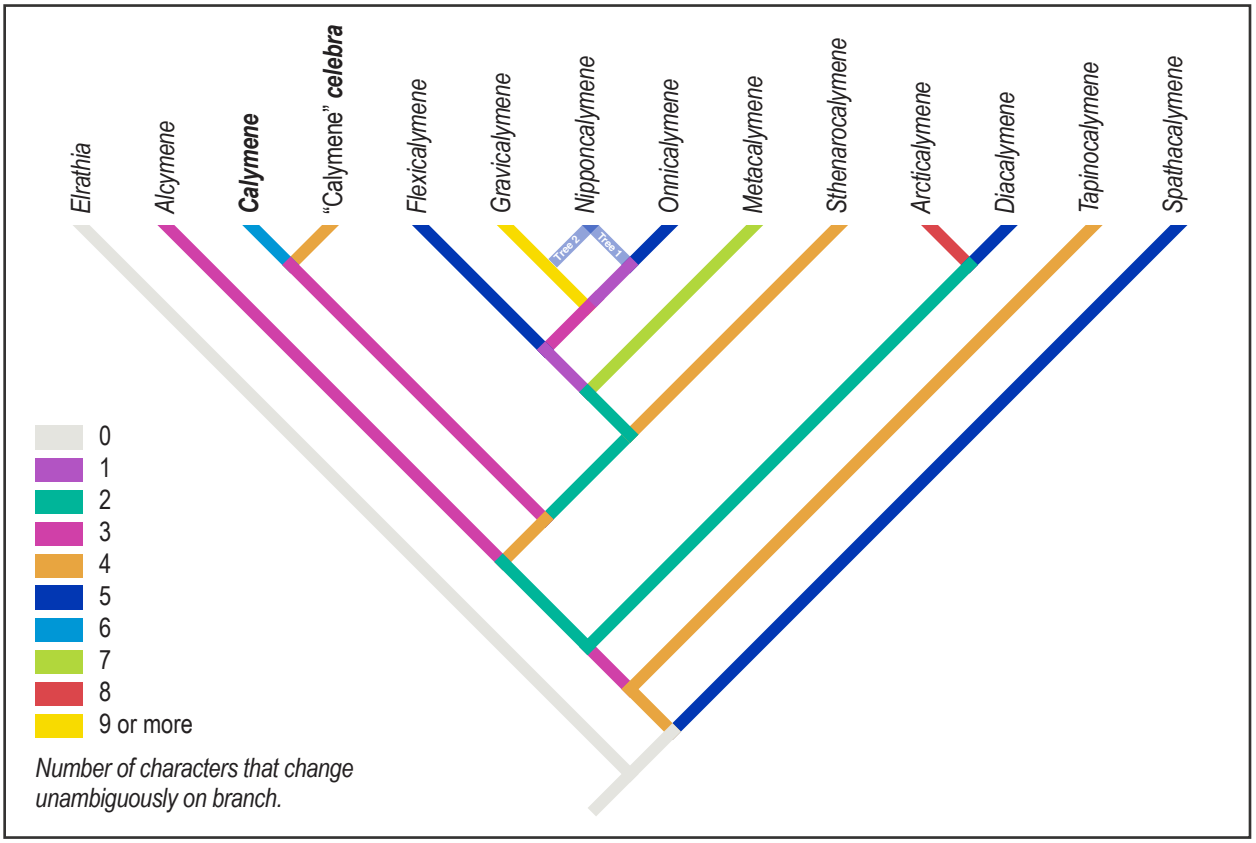

Figure 28. Shortest trees discovered using PAUP (Tree 1 and 2). In Tree 1, *Nipponcalymene* is most closely related to *Onnicalymene*. In Tree 2, *Nipponcalymene* is most closely related to *Gravicalymene*.

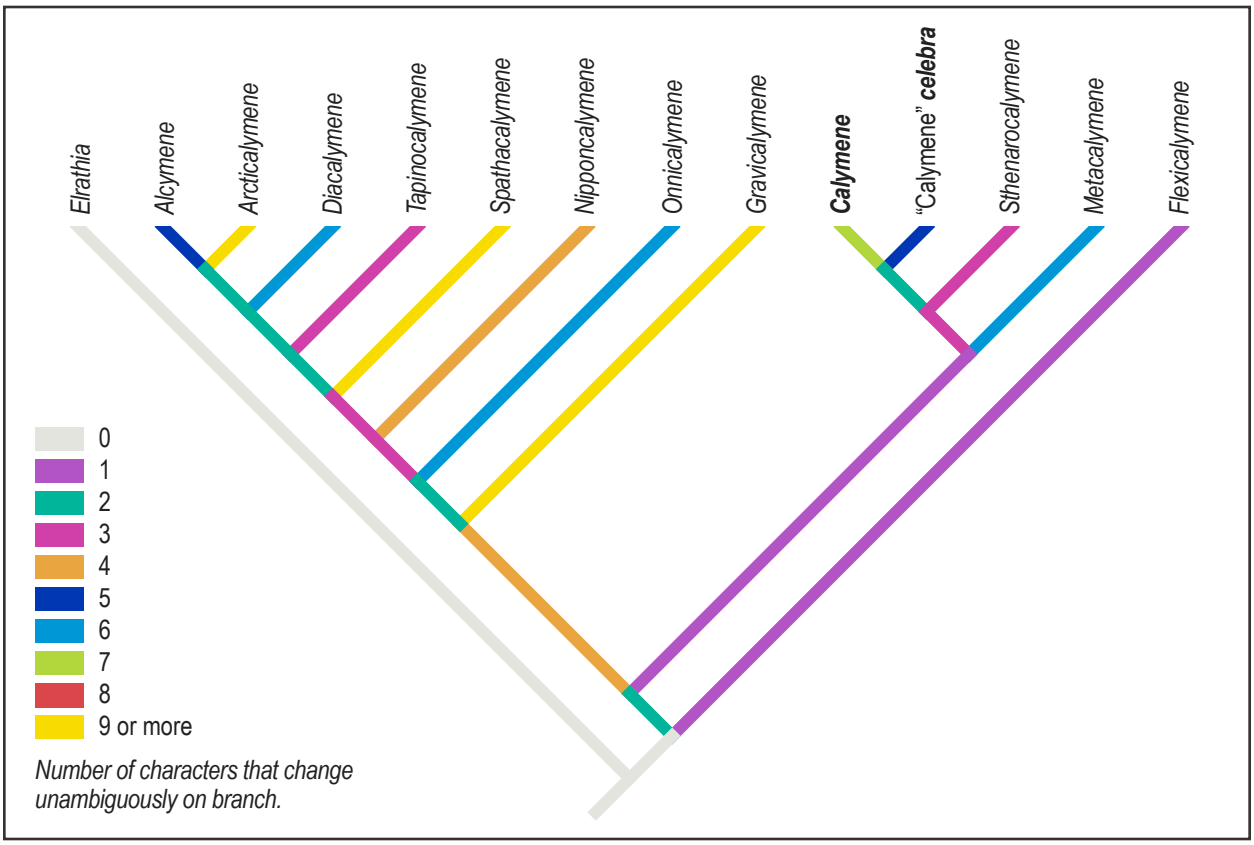

Figure 29. Alternate tree (Tree 3) discovered using PAUP.

Onnicalymene are more closely related to each other than either is to any other form. In Tree 2 (see Figure 28) *Nipponcalymene* and *Gravicalymene* are more closely related to each other. Although evolutionary placement of other study genera varied between the two possibilities, in both cases, "Calymene" *celebra* clusters with *Calymene (C. Blumenbachii)*. Based on these results, "Calymene" *celebra* is more closely related to *C. Blumenbachii* than to the other ingroup taxa, and it is likely that the two species belong to the same genus.

Tree 3 (as shown in Figure 29) more closely resembles the current "state of affairs" – *Calymene* (including *celebra*), *Sthenarocalymene*, *Metacalymene*, and the other trilobites analyzed each has enough character differences to warrant distinction at the genus level.

Landmark Analysis – The purpose of the landmark analysis was two-fold. First, and foremost, to determine if there was a correlation between the evolutionary inference of cladistics and the similarity in shapes via morphometrics; and second, would enough dissimilarity be found among the study set as well as the added species to show that a century of "splitting" species was in excess?

As previously stated, 86 landmark points were located on each study specimen (see Figure 27). The resulting data were fitted using generalized orthogonal Procrustes analysis in the PAST software. Using the Procrustes data, Principal Component Analysis located hypothetical variables – linear combinations of the original variables – which accounted for much of the variance in the data – 87.489% was accounted for in the first three variables in the first data set. From these new hypothetical variables, scatter plots indicating spatial relationships, as well as cluster dendrograms were produced. Scatter plots were created using Singular Value Decomposition, which provides us with a summary of the data structure represented by a symmetrical matrix such as would be obtained from correlations, covariances or distances algorithms. Cluster Analysis dendrograms indicated hierarchical groupings within the multivariate data. Ward's algorithm was used, allowing clustering to be joined with minimal "increase in within-group variance."

The first data set included "Calymene" *celebra* and four of the five genera to which it has been assigned. Since Holloway (1980) deemed *Apocalymene* synonymous to *Sthenarocalymene*, *Apocalymene* was not used in the study. This data set was used corroborate the phylogenetic analysis. In this data set trial, "Calymene" *celebra* more closely matches *Calymene* than the other three study genera to which it has been assigned over the past 100 years. These results are in line with the findings from the phylogenetic analysis (see Figure 30).

The second data set included taxa in the first data set, in addition to species *Calymene niagarensis, Flexicalymene meeki, Flexicalymene senaria,* and *Gravicalymene abbreviata.* It was with the inclusion of these species that an attempt was made to determine both the similarities and differences between these species and their assigned genera. What was found was that "Calymene"

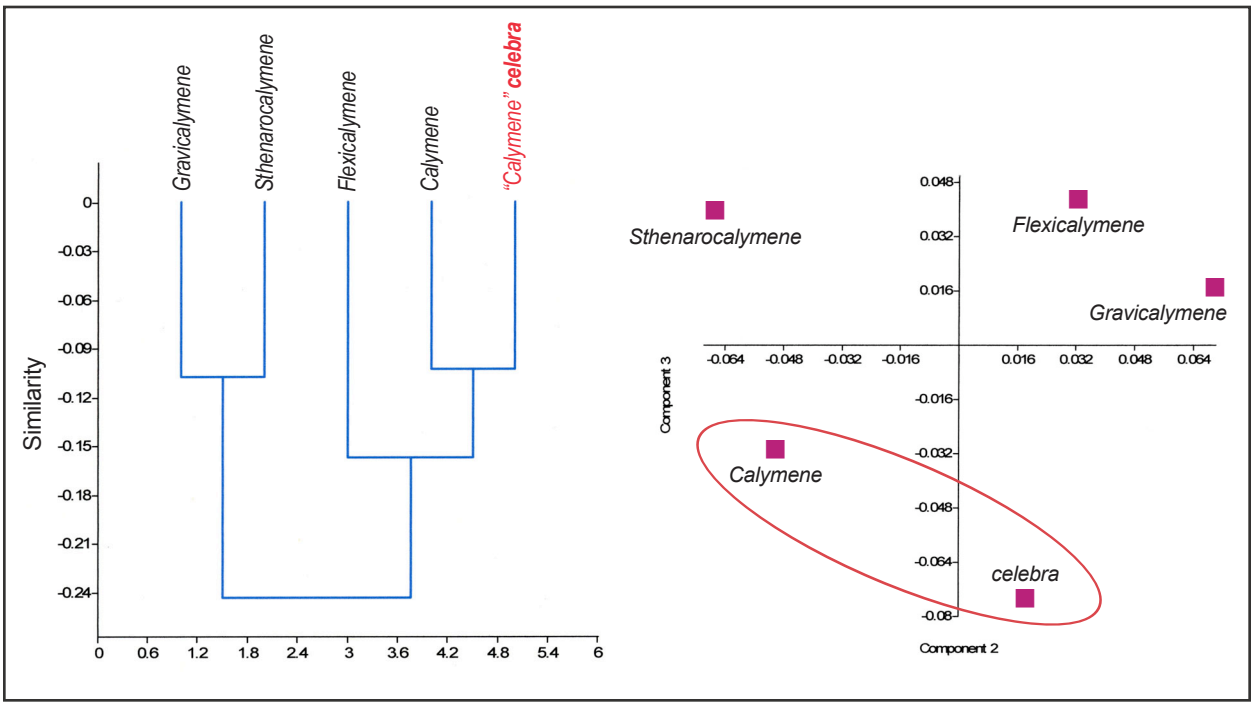

Figure 30. Morphologic similarities among calymenids discovered using Landmark Analysis, as shown in cluster dendrogram and PCA scatter plot.

celebra most closely resembles (clusters with) individual species *Flexicalymene meeki* and *Gravicalymene abbreviata*. but still shares a common cluster – indicating a close similarity – with *Calymene* and *Calymene niagarensis,* It shows less morphologic similarity with *Calymene*, *Calymene niagarensis*, and the type species of *Flexicalymene*, *F. seneria* (see Figure 31). These results support that morphologic variation among calymenid species is considerable, and in some cases, approximating the variation observed at the generic level.

It should be pointed out that there are vast differences in cluster analysis and scatter plots of PCA data. Cluster analysis, although non-statistical, is an explorative technique for identifying groups and subgroups; while PCA is a statistical process that looks at the variance within data. Comparison of the dendrograms and scatter plots can and will show different results. What is surprising so far is that although they show different morphologic similarities between the individual species in the study group, both methods suggest that "Calymene" *celebra* is more similar to, and by

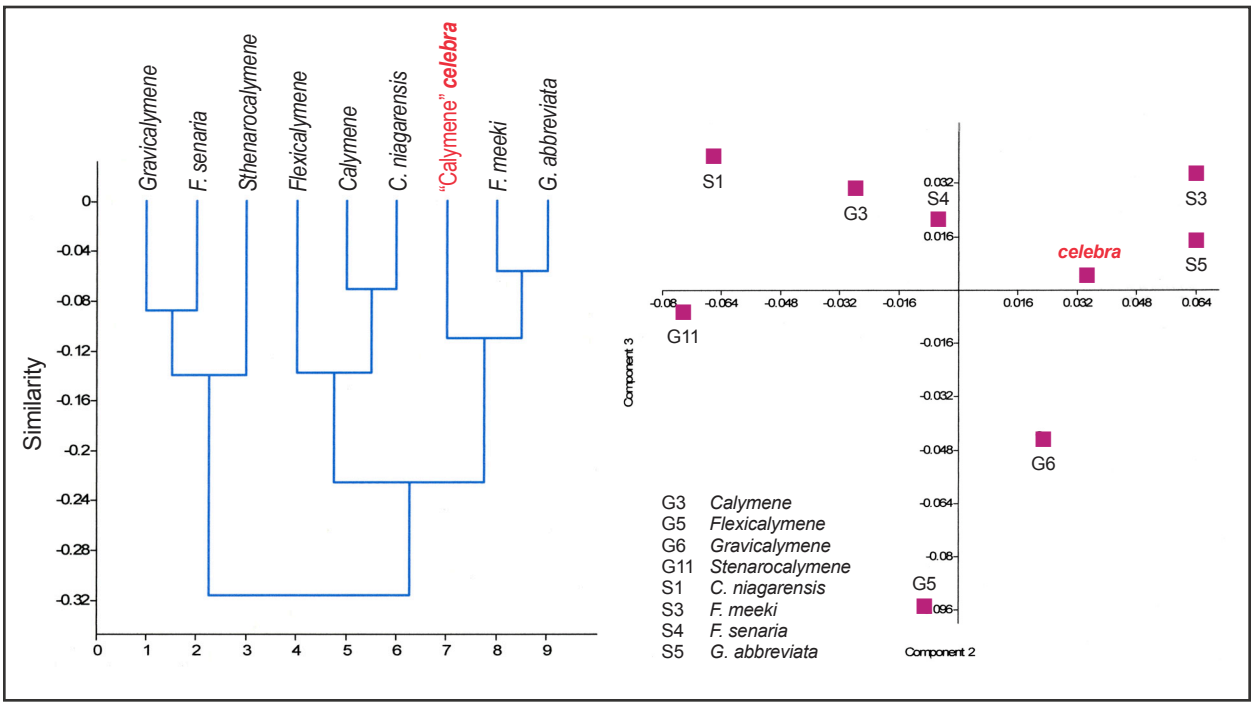

Figure 31. Morphologic similarities among calymenids discovered using Landmark Analysis of the second data set, as shown in cluster dendrogram and PCA scatter plot.

reference, more closely related to *Calymene* than any other genus. As additional species and/or genera are added to the data sets, can equivalent results be expected?

The third data set included the same group as the cladistic analysis – "Calymene" *celebra* and the ingroup genera. The complete Principal Component Analysis was able to account for 83.659% of the variance in the first three components. Because results sometimes differ between component sets, both the first and second, and the second and third component variables, were plotted to assure results. What was found was that in the cluster analysis, "Calymene" *celebra* now shows more similarity with *Gravicalymene* and *Sthenarocalymene*, and shares somewhat fewer similarities with all the of the study genera except *Alcymene, Arcticalymene,* and *Tapinocalymene.* It can again be concluded that there is as much similarity between species as there may be differences, excluding the five previously mentioned (see Figure 32).

The PCA 1 vs. PCA 2 (plotting the first component variable vs. the second component variable) data set three confirms the findings of the cluster analysis. However, it more graphically shows a trend of statistical similarity between "Calymene" *celebra* and the four genera it has been assigned to; and shows "Calymene" *celebra* occupying almost the same "statistical" space as *Calymene* in this data set, which tends to corroborate the cladistic results (see Figure 33). Once the additional variables that are included in the PCA 2 vs. PCA 3 scatter plot are considered, "Calymene" *celebra* nests with both *Flexicalymene* and *Calymene*, indicating again, more similarities than differences between the two genera and "Calymene" *celebra*.

As additional specimens are added, as in the case of data set 4, there is a greater species diversity among the study group. Data set 4 combined all of the ingroup genera and the individual

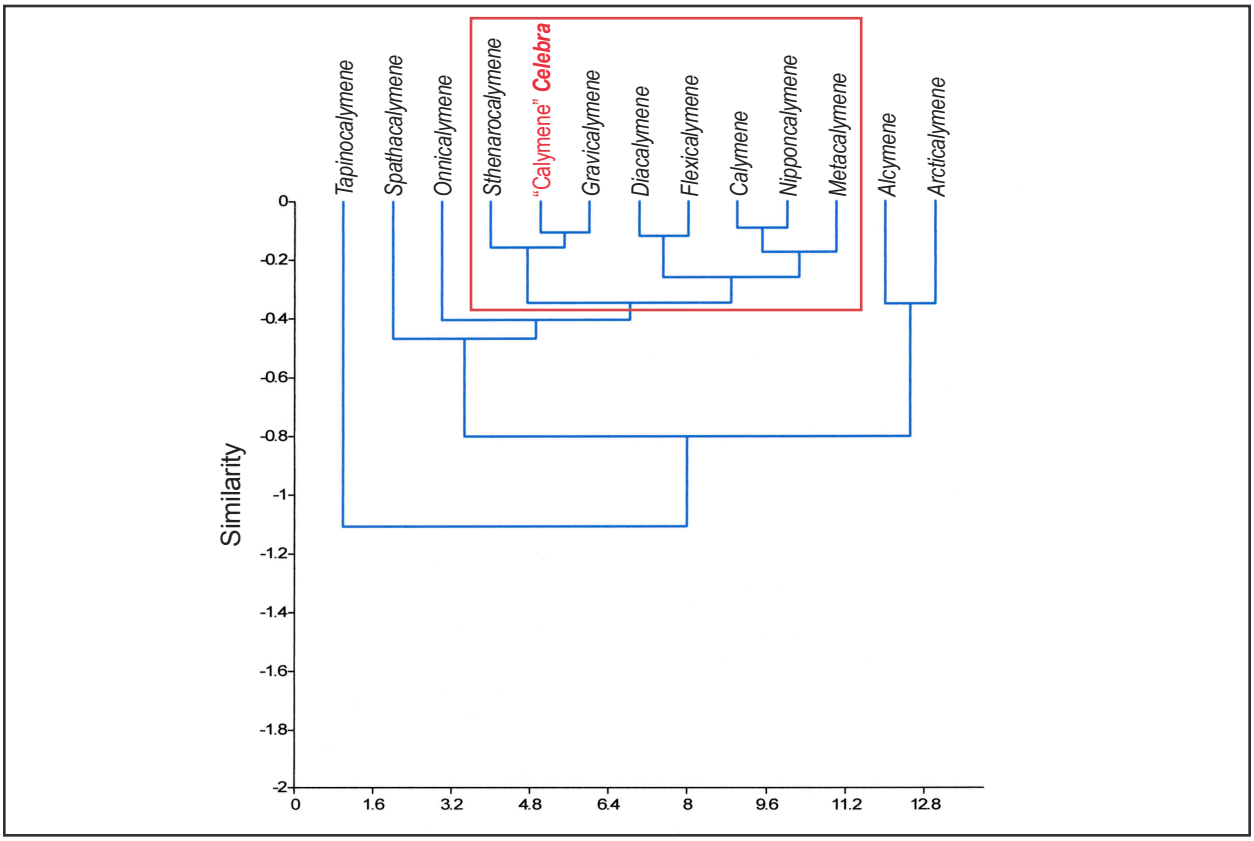

Figure 32. Morphologic similarities among calymenids discovered using Landmark Analysis of the third data set, as shown in cluster dendrogram.

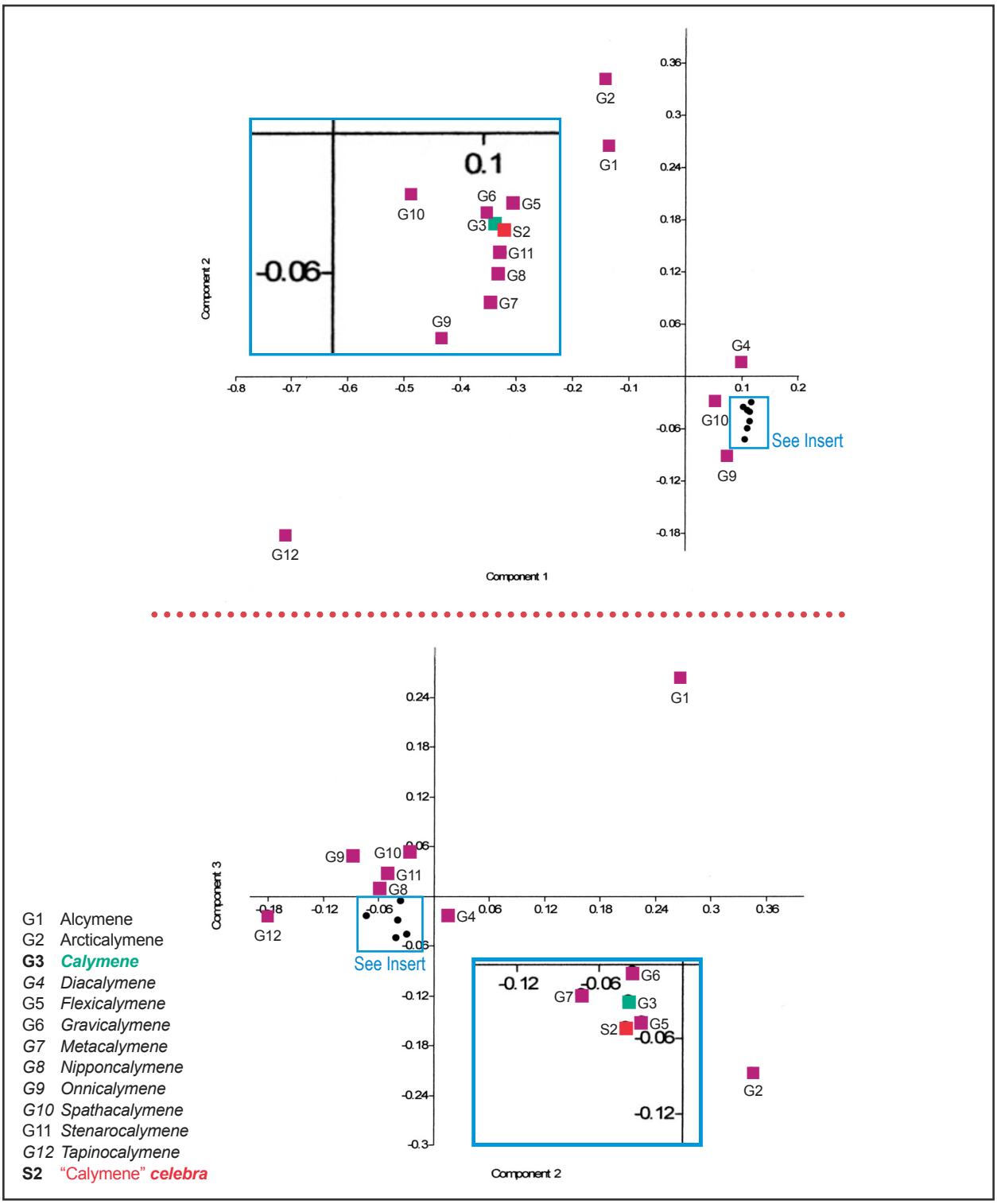

Figure 33. Morphologic similarities among calymenids discovered using Landmark Analysis of the third data set, as shown in PCA scatter plots.

species previously used in Data Set 2. The cluster dendrogram (see Figure 34) from this group shows "Calymene" *celebra* more similar with two other species assigned to different genera. As with the previous cluster, *Alcymene, Arcticalymene, Spathacalymene,* and *Tapinocalymene* are outside of the main cluster, and can be considered different enough to warrant separate generic status. However, the other specimens are too closely nested to warrant individual separate generic assignment.

As specimens are added to the study group, an unconstrained fit would be expected as the software compares more data. A look at the statistical findings of the PCA 1 vs. PCA 2 scatter plot (the PCA 1 vs. PCA 3 plot, and PCA 2 vs. PCA 3 plot were very similar) indicates a nested grouping comprising "Calymene" *celebra, C. niagarensis, Sthenarocalymene, F. senaria, Gravicalymene, Flexicalymene,* and *Calymene* (see Figure 35). In fact, "Calymene" *celebra* and *C. niagarensis* virtually occupy the same statistical space. This is to be expected if in fact, "Calymene" *celebra* belongs to the genus *Calymene*, as the phylogenetic analysis suggests. A smaller nesting of *F. meeki, G. abbreviata, Nipponcalymene,* and *Onnicalymene* just below the former grouping helps corroborate interpretation that the similarities among the calymenids are greater than the differences. It is evident that the species *F. meeki* and *G. abbreviata* are more similar to *Nipponcalymene* and *Onnicalymene* than they are to the type species of their respective genera, and therefore, possibly assigned incorrectly. This suggests the classic dilemma: should genera be defined strictly morphologically (as in the past) [Landmark Analysis], or phylogenetically based on morphologic proxies of shared descent [Cladistic Analysis].

In each of the PCA data sets, "Calymene" *celebra* shares enough statistical similarities with *Calymene* to be placed within that genus. The cluster analysis method, searching for hypothetical groupings, indicates that "Calymene" *celebra* is more closely similar to *Calymene* in the smaller data sets. As the data sets get larger, the cluster data indicates that there is as much, if not more, similarity between the generic groups and the individual species as there are dissimilarities. In some, "Calymene" *celebra* is closer in statistical similarity to species assigned to other genera, that to its own holotype. This too indicates inflation at the generic level.

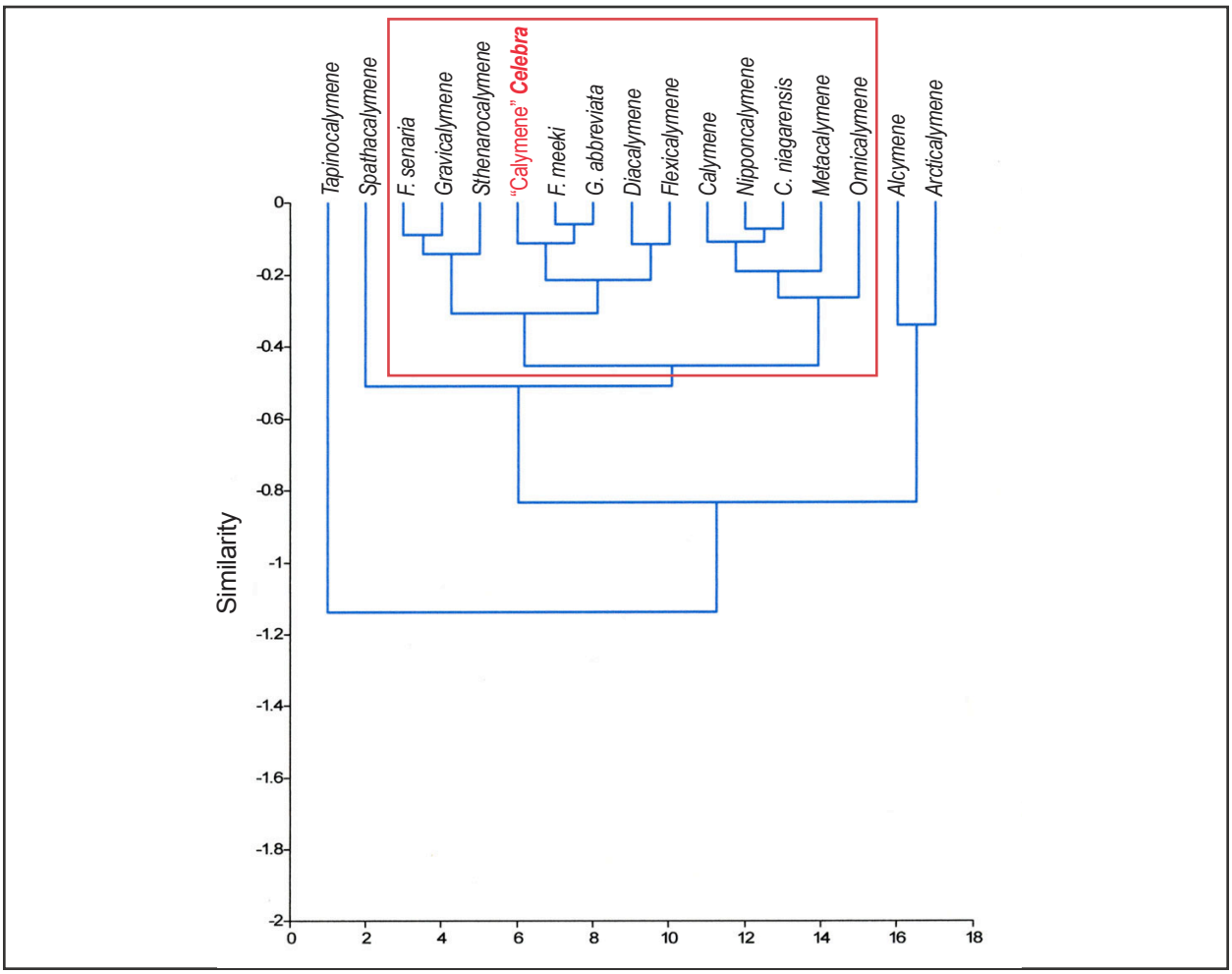

Figure 34. Morphologic similarities among calymenids discovered using Landmark Analysis of the fourth data set, as shown in cluster dendrogram.

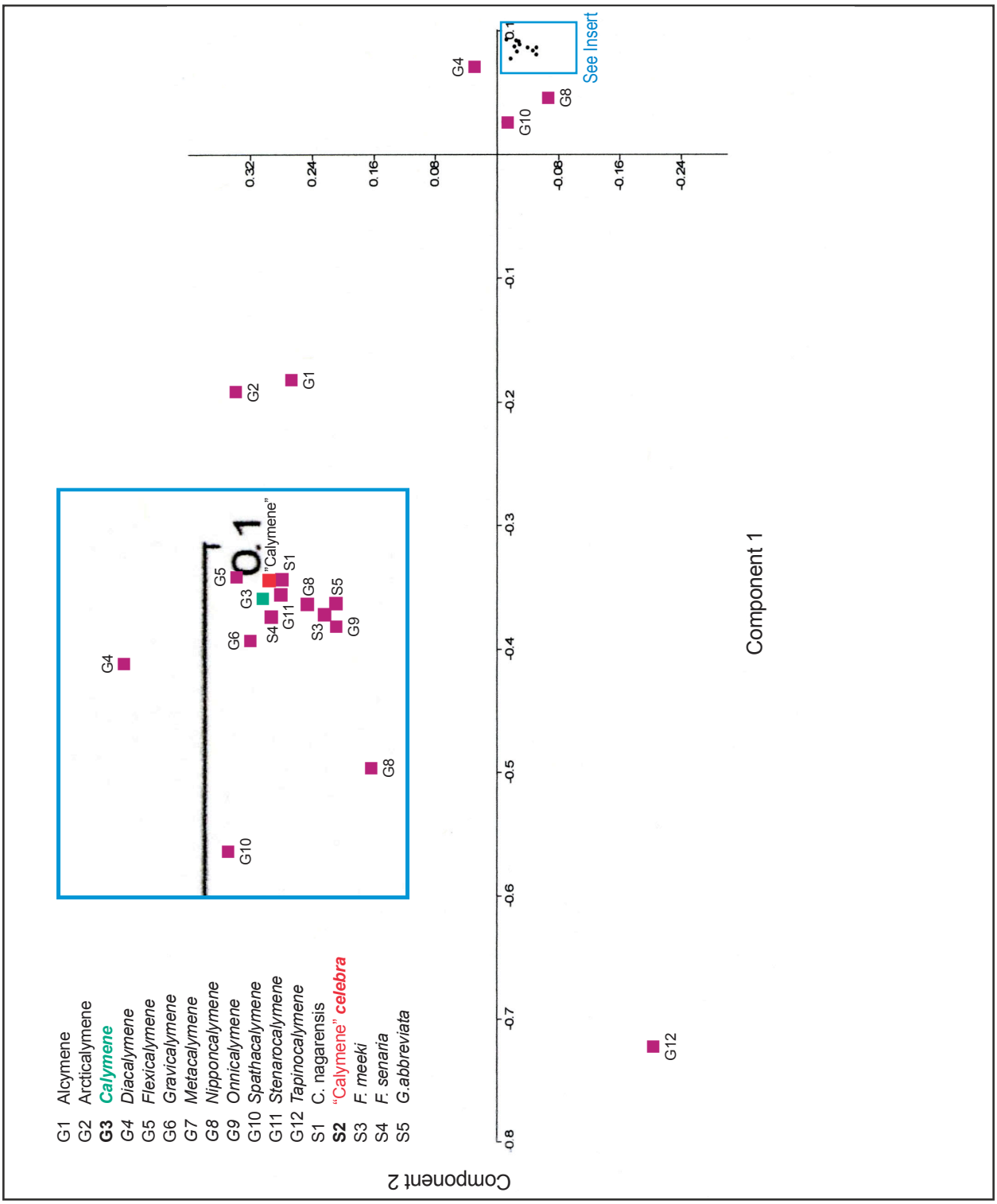

Figure 34. Morphologic similarities among calymenids discovered using Landmark Analysis of the fourth data set, as shown in PCA scatter plots.

CONCLUSION

> "Evolution proceeds in two major modes. In the first, phyletic transformation, an entire population changes from one state to another. …The second mode, speciation, replenishes the earth. New species branch off from a persisting parental stock. … and I believe that speciation is responsible for almost all evolutionary change." (Gould, 1980).

The purpose of this study was to find evidence of speciation among one species, "Calymene" *celebra*, and some of the trilobite genera assigned to the family Calymenidae. Not only was it important to find an evolutionary trend through cladistics, but to show its reliability through the use of statistics. If such a connection could be found and correlated, then we would have gained greater insight into the evolutionary affinities of this "overcrowded" family of trilobites.

Phylogenetic results support inclusion of *celebra* in the genus *Calymene.* A more direct statistical relationship bewteen *celebra* and *Calymene* was found when compared to those genera that *celebra* has been assigned to over the years (see Figure 30). As the data pool is increased by the addition of four species assigned to the study genera – *Flexicalymene senaria*, *Flexicalymene meeki*, *Calymene niagarensis*, and *Gravicalymene abbreviata* (see Figures 14 & 15, page 38) – *celebra* clusters closest with both *F. senaria* and *G. abbreviata,* indicating similarities in their respective morphologies (see Figure 31). However, it still nests closer to the genus *Calymene* than to any of the other four genera it has been assigned to.

When we look at the same data set as used in the cladistic analysis – to include only *celebra* and all genera in the study (see Figure 32) – the results mirror those when *celebra* is compared to all samples in the study (see Figure 34). It was determined that as more samples were added, *celebra*

becomes clustered/nested with different genera and/or species, indicating that the morphological differences between them is not significant enough to warrant generic distinction. Analysis of the scatter plots from the PCA of the study genera and *celebra* (see Figures 33 & 34) show that *celebra* always plots closer to *Calymene* than any other genus. In some analyses, they both share the same statistical space indicating strong statistical similarities. Because of the strong correlation between both type of results, I infer that *celebra* should be assigned to the genus *Calymene*, as first described by Percy Raymond in 1916.

The question remains, what amount of differences warrant recognition of a distinct calymenid trilobite genus. Winston (1999) stated that, "Genera are defined not by one character, but by a group of carefully chosen characters." Mayr and Ashlock (1991 wrote, "In cases where modifications are slight, it is better to revise the genus than to create a completely new genus." This would lead us to think that within the genera *Calymene, Flexicalymene, Apocalymene, Gravicalymene,* and *Sthenarocalymene*, as well as others, the morphological characteristics – and modifications of those characteristics – are slight enough that erection of new genera, as seen over the years, was unwarranted.

While this study just scratched the surface into the genetic affinities of the Calymenidae, enough evidence has come to light that would warrant a full phylogenetic and morphometric revision of the entire family.

WORKS CITED

Adrian, Jonathan M., Edgecombe, Gregory D., and Lieberman, Bruce S., ed. 2001. Fossils, Phylogeny, and Form: An Analytical Approach. Kluwer Academic/Plenum Publishers. New York, NY.

Agassiz, J. L. R. 1857. Essay on Classification. Contributions to the Natural History of the United States. Little Brown. Boston, MA. Vol 1, Part1.

Bartlett, H. H. 1940. The concept of the genus – I. History of the generis concept in botany. Bulletin of the Torrey Botany Club, 67:349-362.

Cain, A. J. 1956. The Genus in Evolutionay Taxonomy. Systematic Zoology, Vol.5, No. 3, pp. 97-109.

Collier-Malone, S. 2004. Stratigraphy, Sedimentology and Palaeontology of a Silurian-age Quarry in Ludlow Falls, Ohio with Classroom Application. [MST Research Project]: Dayton, Ohio, Wright State University, pg. 58.

Crowson, R. A. 1970. Classification and Biology. Heinemann Publishing. London, UK.

Cuvier, G. 1827-35. The Animal Kingdom Arranged in Conformity with Its Organisation. William S. Orr. London, UK. 1:9

Doolittle, W. Ford. 2000. Another branch of the family. New York Times, June 18, 2000.

Elliott, M. D. 1984. Petrology of the Middle Silurian dolomites of Clark and Greene Counties, Ohio. [M.S. thesis]: Dayton, Ohio, Wright State University, 84 p.

Foerste, A. F. 1919. Notes on Isotelus, Achrolichas, Calymene, and Encrinurus: Bulletin of the Scientific Laboratories of Denison University, 19:65-81.

Fortey, R. A. and B. D. E. Chatterton. 1988. Classification of the trilobite suborder Asaphina. Palaeontology, 31:165-222.

Fortey, R. A. 1990. Ontogeny, hypostome attachment and trilobite classification. Palaeontology, 33:529-576.

Fortey, R.A. 1997: Phylogenetic Concepts in the History of Trilobite Classification. Second International Trilobite Conference, Brock University, St. Catharines, Ontario.

Fotey, Richard, in Kaesler, Roger L., ed. 1997. Treatise on Invertebrate Paleontology, Part O, Arthropoda 1. Geological Society of America and University of Kansas Press.

WORKS CITED (CONT'D)

Fortey, Richard, and Droser, Mary L. 1997. Trilobites from the Base of the Type Whiterockian (Middle Ordovician) in Nevada, Papers from the Second International Trilobite Conference. Journal of Paleontology, 73(2):182-20

Fortey, Richard. 2001. Trilobite Systematics: The Last 75 Years. Journal of Paleontology. 75:1141-1151.

Gass, K. C., Edgecomb, G. D., Ramsköld, Lars, Mikulic, D. G., and Watkins, Rodney. 1992. Silurian Encrinurinae (Trilobita) from the central United States. Journal of Paleontology, 66:75-89.

Gould, Stephan Jay. 1977. Ontogeny and Phylogeny. Harvard University Press. Cambridge, MA.

Gould, Stephen Jay 1980. "The Episodic Nature of Evolutionary Change" The Panda's Thumb. New York: W. W. Norton & Co., p. 181-182.

Gould, Stephen Jay. 1989. Wonderful Life. W. W. Norton and Company, Inc. New York, NY.

Hall, J., and R. P. Whitfield. 1877. Paleontology. United States Geological Exploration for the Fortieth Parallel 4(2): 198-302.

Hammer, Øyvind, and Harper, David A. T. 2006. Paleontological Data Analysis. Blackwell Publishing. Malden, MA.

Hughes, Nigel C. 1995. Trilobite Taphonomy and Taxonomy: A Problem and Some Implications. Palaios, 10:283-285.

Hupé, Pierre. 1954. Classification des trilobites. Annales de Paléontologie 39:61-168.

Hupé, Pierre. 1955. Classification des trilobites. Annales de Paléontologie 41:91-325.

Hupé, Pierre. 1954. À propos des organes de Pander ded trilobites. Bulletin de la Société Géologique de France (series 6) 4:701-711.

Jell, P. A. and Adrian, J. M. 2003. Available Generic Names for Trilobites, Memoirs of the Queensland Museum, 48:331-553

Just, T. 1953. Generic synopses and modern taxonomy. Chronica Botanica, 14:103-114.

Harrington, H. J., in Moore, Raymond C., ed. 1959. Treatise on Invertebrate Paleontology, Part O, Arthrpoda 1. Geological Society of America and University of Kansas Press.

WORKS CITED (CONT'D)

Kaesler, Roger L., ed. 1997. Treatise on Invertebrate Paleontology, Part O, Arthrpoda 1. Geological Society of America and University of Kansas Press. Boulder, CO and Lawrence, KS.

La Rocque, Aurèle, and Marple, M. F. 1955. Ohio Fossils. Ohio Division of Geological Survey Bulletin 54.

Levi-Setti, Riccardo. 1993. Trilobites. Second Edition. The University of Chicago Press. Chicago, IL. ISBN 0-226-47452-6.

Ludvigsen, Rolf. 1979. Fossils of Ontario, part 1: The trilobites. Royal Ontario Museum Life Sciences Miscellaneous Publications.

Lyttelton, C. 1752 (in Mikulic, Donald G., and Kluessendorf, Joanne. 2007). A letter from the Rev. Charles Lyttelton LL.D. and ERS., Dean of Exeter, to the President, concerning a non-descript petrified insect [Dec. 20, 1750]: Philosophical Transactions of the Royal Society of London, v. 46 (for the years 1749 and 1750), p. 598, 599. (Extract of a Letter from the Rev. Dr. Lyttelton to C. Mortimer, Secret. R. S., p. 600.)

Maddison, David R., and Maddison, Wayne P. 2008. MacClade, Version 4.08 software. Sinauer Associates, Inc., publishers. Sunderland, MA.

Mendez da Costa, E. 1809. On the fossil found at Dudley in Staffordshire, and described in the Phil. Trans. No. 496: Philosophical Transactions of the Royal Society of London, from their commencement in 1665, to the year 1800; Abridged, with notes and biographic illustrations, v. X, from 1750 to 1755, p. 401.

Mortimer, C. 1756 (in Mikulic, Donald G., and Kluessendorf, Joanne. 2007). Some further account of the before mentioned Dudley Fossil; by the Editor of these Transactions. Philosophical Transactions of the Royal Society of London (from the year 1743, to the year 1750), Abridged, v. 10, chap. 3, art. XXVII, p. 656, 657.

Panchen, Alec L. 1992. Classification, Evolution and the Nature of Biology. Cambridge University Press. Cambridge, UK.

Raw, Frank. 1953. The External Morphology of the Trilobite and its Significance. Journal of Paleontology, 27:82-129.

MacLeod, Norman, and Forey, Peter L., ed. 2002. Morphology, Shape and Phylogeny. Taylor & Francis. London, England.

Mikulic, D. G. 1981. Trilobites in Paleozoic carbonate buildups. Lethaia, V. 14:45-56.

WORKS CITED (CONT'D)

Mikulic, Donald G., and Kluessendorf, Joanne. 2007. Legacy of the Locust – Dudley and its Fabulous Trilobite, in Fabulous Fossils – 300 Years of Worldwide Research on Trilobites. New York State Museum Bulletin 507. The University of the State of New York. 141-169.

Moore, Raymond C., ed. 1959. Treatise on Invertebrate Paleontology, Part O, Arthropoda 1. Geological Society of America and University of Kansas Press.

Raup, David M. and Stanley, Steven M. 1978. Principles of Paleontology. New York, W. H. Freeman and Company.

Simpson, G. G. 1961. Principles of Animal Taxonomy. New York, Columbia University Press.

Stevens, P. F. 1994. The Development of Biological Systematics: Antoine-Laurent de Jussieu, Nature and the natural System. New York, Columbia University Press.

Stout, W. 1941. Dolomites and Limestones of Western Ohio Ohio Geological Survey Bulletin, 42:468.

Swafford, David L. 2002. PAUP: Phylogenetic Analysis Using Parsimony, Ver. 4.0 software. Sinauer Associates, Inc., publishers. Sunderland, MA.

Svenson, H. K. 1945. On the descriptive method of Linneaeus. Rhodora, 47 (562):273-302 and (563):363-388.

Trudge, Colin. 2000. A variety of life: A Survey and a Celebration of All the Creatures That Have Ever Lived. Oxford University Press. United Kingdom.

Whittington, H. B. 1971. A new calymenid trilobite from the Maquoketa Shale, Iowa. Smithsonian Contributions to Paleobiology 3: 129-136.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology, 27:17-26.

Wiley, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. New York, Wiley.

REFERENCE MATERIALS

Adrian, Jonathan M. 2001. Systematic Paleontology, Journal of Paleontology. 75:1055-1057

Adrian, Jonathan M., and Edgecombe, G. D. 1997. Silurian (Wenlock) calymenid trilobites from the Cape Phillips Formation, central Canadian Arctic, Journal of Paleontology 71: 657-682.

Barrande, J. 1846. Notice préliminaire sur le système Silurien et les Trilobites de Bohême, (Hirschfeld: Leipzig).

Barrande, J. 1846. Nouveaux Trilobites. Supplément à la Notice préliminaire sur le système Silurien et les Trilobites de Bohême. (Calve: Prague).

Bergeron, J.N. 1890. Sur une forme nouvelle de Trilobite de la famille des Calymenidae (genre Calymenella), Bulletin de la Société Géologique de France 18: 365-371.

Bookstein, F. L. 1991. Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge University Press, Cambridge, UK.

Brongniart, A. 1822. Les Trilobites., In Brongniart, A. & Desmarest, A.-G., Histoire naturelle des crustacés fossiles, sous les rapports zoölogiques et géologiques. (Paris & Strasbourg), 1822.

Carroll, Sean B. 2005. Endless Forms Most Beautiful. W. W. Norton and Company, Inc. New York, NY.

Cracraft, Joel. 2004. Editor, Assembling the Tree of Life, Oxford University Press, New York, NY, ISBN 0-19-517234-5

Curtis, N. J., and Lane, P. D. 1997. The Llandovery trilobites of England and Wales: Part 1, Monographs 605: 1-50.

Dean, W. T. 1967. The correlation and trilobite fauna of the Bedinan Formation (Ordovician) in southeastern Turkey, Bulletin of the British Museum (Natural History), Geology Series 15: 81-123.

Dean, W. T. 1962. The trilobites of the Caradoc Series in the Cross Fell Inlier of northern England, Bulletin of the British Museum (Natural History), Geology Series 7: 65-134.

Desmarest, A-G. 1816. *Calymene*, in Biot, J. B., et aI., editors. Nouveau Dictionnaire d'Histoire NatureIJe, 2nd edition, v. 5, p. 49, 50: Paris, Detterville.

Desmarest, A-G. 1817. Crustaces Fossiles, in Biot, J. B., et aI., editors, Nouveau Dictionnaire d'Histoire Naturelle, 2nd edition, v. 8, p. 495-518: Paris, Detterville.

Duncan, Thomas, and Stuessy, Tod F. 1984. Editors, Cladistics: Perspectives on the Reconstruction of Evolutionary History, Columbia University Press, New York, NY, ISBN 0-231-05430-0

Duncan, Thomas, and Stuessy, Tod F. 1985. Editors, Cladistic Theory and Methodology, Van Nostrand Reinhold Company, New York, NY, ISBN 0-442-21845-1

Feldman, Rodney M. 1996. Editor-In-Chief, Bulletin 70: Fossils of Ohio, Ohio Department of Natural Resources, Division of Geological Survey, Columbus, OH, ISBN 0-931079-05-5

Felsenstein, Joseph. 2004. Inferring Phylogenies, Sinauer Associates, Inc, Sunderland, MA, ISBN 0-87893-177-5

Forey, P. L., Humphries, C. J., Kitching, I. L., Scotland, R. W., Siebert, D. J. and Williams, D. M. 1992. Cladistics – A Practical Course in Systematics, Clarendon Press, Oxford, ISBN 0-19-857766-4

Fortey, R. A., and B. D. E. Chatterton. 1988. Classification of the trilobite suborder Asaphina. Paleontology, 31:165-222.

Fortey, Richard. 2000. Trilobite: Eyewitness to Evolution, Random House, New York, NY.

Fortey, Richard. 2001. Trilobite Systematics: The Last 75 Years, Journal of Paleontology, 75:1141-1151.

Hammann, W. 1977. Neue Calymenacea (Trilobita) ausdem Ordovizium von Spanien, Senckenbergiana lethaea 58: 91-97.

Hammann, W. & Leone E. F. 1997. Trilobites of the post Sardic (Upper Ordovician) sequence of southern Sardinia – Part 1, Beringeria 20:1-217.

Hall, J. 1861. Report of the Superintendent of the Geological Survey, Wisconsin, (Madison, Wisconsin).

Hey, Jody. 2004. Genes, Categories, and Species – The Evolutionary and Cognitive Causes of the Species Problem, Oxford University Press, New York, NY, ISBN 0-19-514477-5

REFERENCE MATERIALS (CONT'D)

Hicks, H., 1873. On the Tremadoc rocks in the neighbourhood of St. David's, South Wales, Quarterly Journal of the Geological Society of London 29:39-52.

Humphries, Christopher J., and Parenti, Lynn R. 1999. Cladistic Biogeography – Interpreting Patterns of Plant and Animal Distributions, Second Edition, Oxford University Press, Oxford, ISBN 0-19-854818-4

Kaneko, A. 1985. A Middle Devonian trilobite fauna from the Kitakami Mountains, northeast Japan, The Calymenidae. Transactions and Proceedings of the Palaeontological Society of Japan, N.S. 138:94-110.

Kegel, W. 1927. Über obersilurische Trilobiten aus dem Harz und dem Rheinischen Schiefergebirge, Jahrbuch der Preussischen Geologischen Landesanstalt 48:616-647.

Kobayashi, T. 1951. On the Ordovician trilobites in central China, Journal of the Faculty of Science of the Imperial University of Tokyo, section 2: Geology 8(1):1-87.

Kobayashi, T. 1951. On the late Upper Cambrian (Fengshanian) fauna in eastern Jehol, Transactions nd Proceedings of the Palaeontological Society of Japan, new series, 3:75-80, pl. 7.

Kobayashi, T. 1960. Some Ordovician fossils from East Tonkin, Viet Nam, Japanese Journal of Geology and Geography 31:39-48.

Lemen, Cliff A. and Freeman, Patricia W. 1984. The Genus: a Macroevolutionary Problem. Evolution 38(6), pp. 1219-1237.

Lindström, G. 1885. Förteckning pa Gotlands Siluriska Crustacéer, Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 6: 37-100.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species cum Charateribus, Differentiis, Synonymis, Locis. Tomus 1 10th edn. Laurentii Salvii. Halmiae.

Liu, Yeren. 1982. [Trilobita], In [The Palaeontological Atlas of Hunan]. Ministry of Geology and Mineral Resources: Geological Memoirs, Series 2 – Vol. 1, Geological Publishing House: Beijing.

Maksimova, Z. A. 1978. [Some new Devonian trilobites]. Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva 21:94-109.

Maksimova, Z. A. 1968. [Middle Palaeozoic trilobites of central Kazakhstan]. Trudy Vsesoyuznogo Nauchno Issledovatel'skogo Geologicheskogo Instituta (VSEGEI), New Series 165: 1-208.

Mansuy, H. 1908. Contribution a la Carte Géologique de l'Indochine, Palaeontologie, (Service de Mines: Honoi-Hai-Phong) 73p, 18pls.

Moore, Raymond C., ed. 1959. Treatise on Invertebrate Paleontology, Part O, Arthrpoda 1, Geological Society of America and University of Kansas Press.

Murchison, R. I. 1839. The Silurian System, (London).

Novacek, Michael J., and Wheeler, Quentin D. 1999. Extinction and Phylogeny, Columbia University Press, New York, NY, ISBN 0-231-07438-7

Perner, J. 1900. Miscellanea silurica Bohemiae, Palaeontographica Bohemiae 5:1-16.

Raup, D. M. 1966. Geometric analysis of shell coiling: General problems. Journal of Paleontology, 40:1178-90.

Raymond, P. E. 1916. New and old Silurian trilobites from southeastern Wisconsin, with notes on the genera of the Illaenidae, Bulletin of the Museum of Comparative Zoology, Harvard 60: 1-41, 1916.

Reed, F. R. C. 1917. Ordovician and Silurian fossils from Yunnan, Memoirs of the Geological Survey of India. Palaeontologia Indica, N. S. 6:1-84.

Ross, R. J., Jr. 1967. Some Middle Ordovician brachiopods and trilobites from the Basin Ranges, western United States, United States Geological Survey Professional Paper 523-D:1-43.

Rouault, M. 1847. Extrait du Mémoire sur les Trilobites du Département d'Ille-et-Villaine, Bulletin de la Société Géologique de France 4:309-328.

Rouault, M. 1851. Mémoire sur le terrains paléozoiques des environs de Rennes, Bulletin de la Société Géologique de France 8:358-399.

Richter, R. and Richter, E. 1954. Die Trilobiten des Ebbe-Sattels und zu vergleichende Arten. (Ordovizium, Gothlandium /Devon). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 488:1-76.

Shirley, J. 1936. Some British trilobites of the family Calymenidae, Quarterly Journal of the Geological Society of London 92:384-422.

Siveter, D. J. 1977. The Middle Ordovician of the Oslo Region, Norway – Trilobites of the family Calymenidae, Norsk Geologisk Tidsskrift 56:335-396.

Siveter, D. J. 1980. Evolution of the Silurian trilobite *Tapinocalymene* from the Wenlock of the Welsh Borderlands, Palaeontology 23:783-802.

Tomczykowa, E. 1970. Silurian *Spathacalymene* Tillman, 1960 (Trilobita) from Poland, Acta Palaeontologica Polonica 15:63-88.

Tomczykowa, E. 1991. Upper Silurian and Lower Devonian trilobites of Poland, Prace Panstwowego Instytutu Geologicznego 134:1-62.

Ulrich, E.O. 1879. Description of a trilobite from the Niagara Group of Indiana, Journal of the Cincinnati Society for Natural History 2(3):131-134.

Vanuxem, L. 1842. Geology of New York III: Survey of the Third Geological District, Natural History of New York, 1-306.

Walch, J. E. 1771. Die Naturgeschichte der Versteinerungen, Dritter Theil: Nümberg, Paul Johnathon Felstecker, 235 p.

Wicander, Reed, Monroe, James S. 2000. Historical Geology: Evolution of Earth and Life Through Time, Brooks/Cole Publishers, Pacific Grove, CA, ISBN 0-534-37380-1

Winston, Judith E. 1999. Describing Species, Columbia University Press, New York, NY, ISBN 0-231-06824-7